BEHAVIOR OF ORGANISMS

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BEHAVIOR OF ORGANISMS

Activities may accomplish nutrition, respiration, excretion, protection, reproduction, cleansing, organization, rest, or elimination of harmless irritation. Also, behavior may produce immediate pleasure, and the performance of activities may—through remote relationship—be prerequisite to life functions. Some activities carry out more than one function. A few activities are evidently not adaptations to any function. They may be regarded as blind activities unless they are discovered to be adaptations.

This treatise presents an ecological classification of behavior. It is concerned with discrepancies that occur in comprehension, interpretation, and measurement of activities, and serves as an index to important literature. The author is indebted to Professors V. E. Shelford, S. C. Kendeigh, and A. S. Pearse for aid in clarifying parts of this material.

PRINCIPAL ECOLOGICAL ACTIVITIES

Subdivisions within each categorical level under capital letters are practically equivalent. They are to be regarded as ecological equivalents. Locomotion and anchorage have evolved in relation to more than one function. Many treatises cited are important for their bibliographies as well as their texts. Some of these are especially valuable as general references (e.g., Pearse 1939, Warden *et al.* 1935-40, Shelford 1929, Allee 1931, Elton 1935).

I. Nutritive behavior. It is convenient to consider water as a food when it is absorbed through digestive systems and/or when it is used after intake in connection with release or energy from food.

A. Activities that make food available in habitats (Fig. 1).
 1. Migration (locomotion, Fig. 9) and habitat selection (Wetmore 1926, Lincoln 1939, Allen 1939).
 2. Defense of territory (Howard 1929, Kendeigh 1941, Nice 1941).
 3. Storage of food.
  a. Storage in physical niches as occurs for most ants; usually involves construction of niches (Wheeler 1910, Forel 1928).
  b. Storage in plant niches as carried out by woodpeckers; involves construction of niches (Jordan & Kellogg 1922).
  c. Storage in animal niches as occurs for honey ants (Wheeler 1910).
  d. Taking care of commensals such as those that secrete food. For example, some species of ants keep aphids (Wheeler 1910, Forel 1928).
 4. Agriculture and animal culture; practiced by humans and some species of ants (Wheeler 1910).
 5. Keeping slaves that obtain food as occurs for certain species of ants (Wheeler 1910).
 6. Employment of adherence mechanisms such as (1) release of odor-producing chemicals, (2) display of color and form, (3) production of light, and (4) use of trap mechanisms (Fig. 6).
 7. Employment of anchorage mechanisms (Fig. 8). Through growth and differentiation, Bryozoa and most large plants obtain anchor-
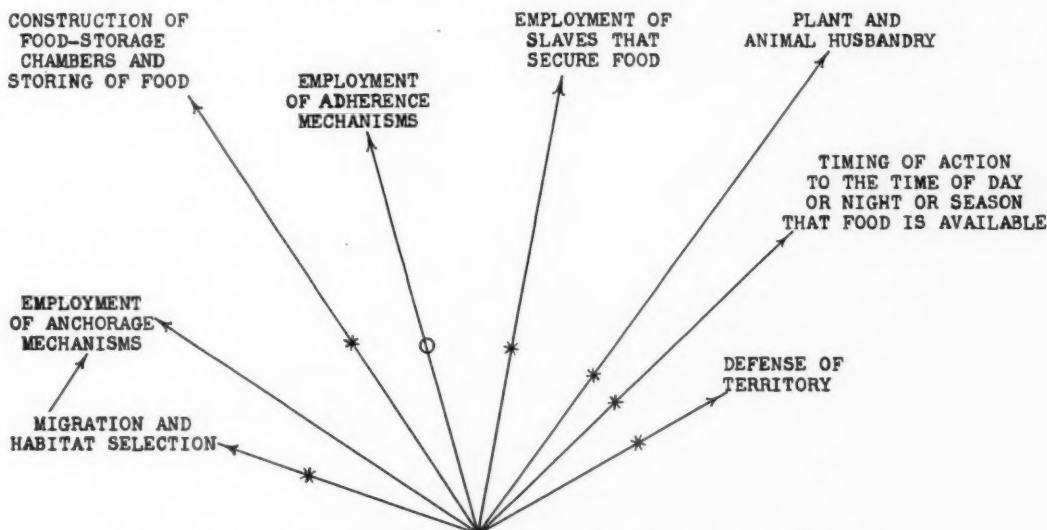

FIG. 1. Making food available in habitats. Locomotion involved*. Anchorage involved°.

age. Anchorage keeps organisms within environments in which food is available. Most spermatophytes employ anchorage mechanisms as part of their food contact apparatus. The same holds true for such parasites as Sacculina.

8. Timing activity to the nychthemeral or seasonal period in which food is available (Elton 1925).

B. Procurement of food (Figs. 2 and 3). Procurement does not pertain to the act of eating. Food accepted may be organic and nonliving (saprophagy or saprophytism), or living (vitophagy), or may consist of both living and nonliving substance (saprovitophagy). Animals may feed upon plants (phytivorism), upon animals (carnivorism), or they may eat both plants and animals (omnivorism). Parasitism is a form of phytivorism or carnivorism and is characterized by the slow consumption of the tissues, fluids, or food stores of living organisms.

1. Active securement of food by means of trap, separator, or excavating mechanisms. Locomotion or anchorage is involved. In this category, organisms are self-dependent at least to some extent. Traps are constructed through dynamic activity in some instances.

a. Independent procurement.
  (1) Capture of food.
  (2) Union with hosts (parasitism and commensalism) in those instances in which union is carried out via activity of the parasite or active commensal. Anchorage or excavating mechanisms are involved, and locomotion may be involved as applies to cercariae.

b. Partial dependency upon other individuals and partial reliance upon locomotion.
  (1) Robbery.
    (a) Robbing other individuals of food that they hold or possess in food stores. Jaegers, gulls, and eagles are known to rob other birds of their catch of fish (Allen 1925). Some guests of ants and termites rob their hosts of food (Donisthorpe 1927, Emerson 1935, cf., 1938).
    (b) Poaching. Foraging in the territories of other individuals or colonies as occurs among birds (Nice 1941, Kendeigh 1941).
  (2) Sycophantism, inquilinism, or gleaning as illustrated by Remora (Borradaile 1923). This type of behavior is characterized by the gathering of food that
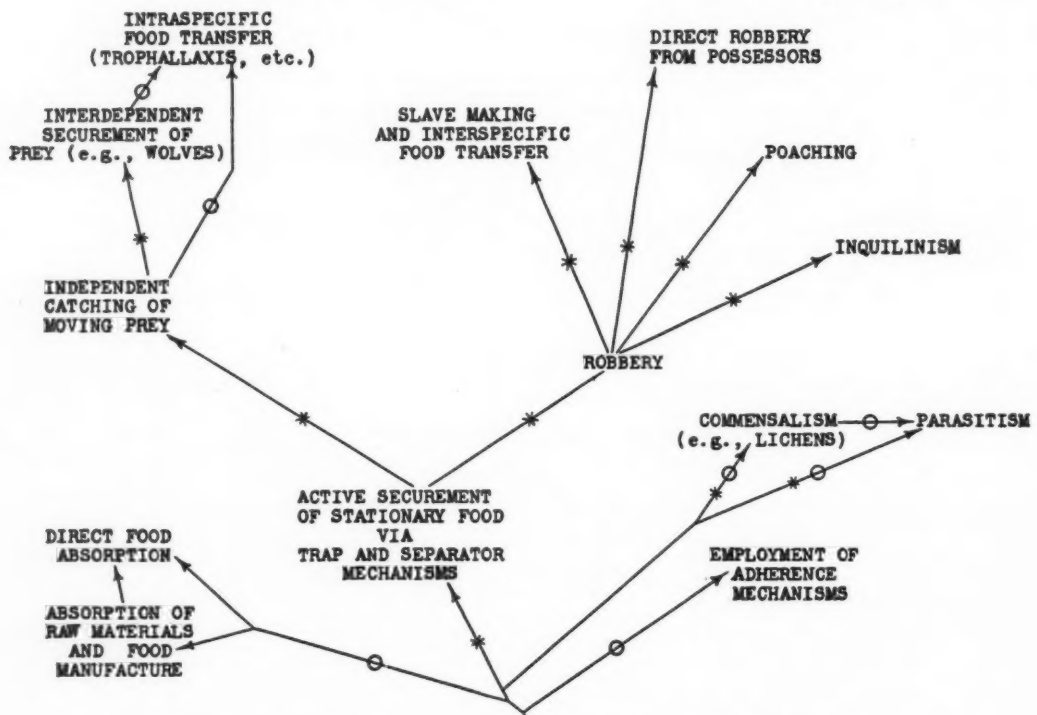

Fig. 2. Procurement of food. Locomotion involved*. Anchorage involved°.

is discarded by animals. Some of the feeding of certain scavengers such as hyenas belongs in this category.

    (3) Interdependent procurement. Coöperative predation illustrated by wolves as they form into packs when attacking prey (Hammerton 1930).

2. Passive procurement of food. Dependency upon other individuals for food procurement.

    a. Intraspecific food transfer as illustrated by the acceptance of food from adults by immature altricial birds (Allen 1925, 1930).

    b. Parasitism and commensalism in those instances in which dependents are eaten by their hosts or are presented with food by their hosts; occurs for cowbirds (Allen 1925), for ants that are fed by slaves (Forel 1928), for other insects that are fed by hosts (Donisthorpe 1927, Emerson 1935, cf., 1938), and for many parasites (Chandler 1940, Pearse 1942, Hegner *et al.* 1938).

C. Feeding. Eating.

1. Absorption, as occurs for the venus fly-trap and many parasites. Growth and consequent increase in absorptive surface is involved as for trees and Sacculina.

2. Protoplasmic engulfment.

    a. Immediate formation of food vacuoles; occurs for Amoeba.

    b. Gradual formation of food vacuoles; occurs for Paramecium.

3. Swallowing (Fig. 3).

D. Making room for food.

1. Regurgitation; occurs for Hydra.

2. Defecation.

3. Regurgitation plus defecation; occurs for owls (Allen 1925).

4. Absorption of food only; occurs for antlions (Comstock 1930).

II. Respiratory behavior, with especial regard to aquatic animals (Fig. 4).

A. Activities that make oxygen available in the general habitat.

1. Migration (locomotion) upstream and habitat selection (Shelford 1937, pp. 106, 110-113).

2. Employment of anchorage mechanisms as by aquatic animals that live in rapids; for example, Parnidae (Fig. 8) (Lutz 1918, Pearse 1939, p. 317).

B. Procurement of air (oxygen).

1. Breathing movements. For instance: inspiration and expiration by means of pumps including abdominal respiratory movements in connection with intestinal respiration of dragon-fly nymphs and tracheal respiration of bees and flies; gill movements; manipulation of respiratory valves by fishes; etc.
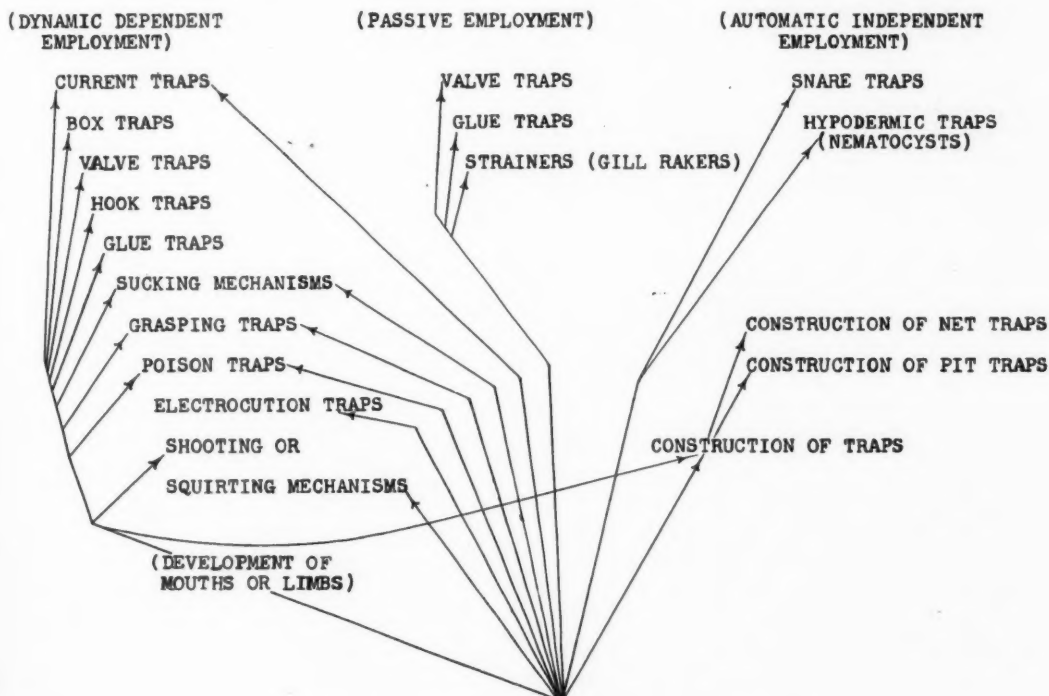

FIG. 3. Trap mechanisms and separator mechanisms.

2. Air trapping.
   a. In down; occurs for Hydrophilus, Noto-
      necta, Argyroneta (Borradaile 1923).
   b. In external reservoirs; for instance, collec-
      tion of air under forewings or plates by
      aquatic bugs and beetles (Borradaile 1923,
      Needham & Lloyd 1928).
   c. In internal reservoirs such as lungs or
      trachea. This type of air trapping occurs
      for turtles, whales, and mosquito larvae.
      Air trapping, conveyance, and storage oc-
      cur for water lilies.
3. Use of extension tubes as by Ranatra, Nepa,
   and Eristalis.
4. Locomotion (involved in obtainment of oxy-
   gen, as occurs for mosquito larvae, aquatic
   beetles, Corixidae, Notonectidae, and Belosto-
   matidae) plus air trapping (Comstock 1930).
5. Construction of an air chamber for self,
   mate, eggs, and young as illustrated by
   Argyroneta (Borradaile 1923, p. 250).
6. Tapping of oxygen from plants as occurs for
   Donacia (Carpenter 1928, p. 56).
7. Anaerobiosis as occurs for some kinds of
   bacteria.
8₁. Diffusion in such animals as Amoeba.
8₂. Diffusion assisted by oscillatory movements
    of the whole body or by locomotion as occurs
    for some Diptera larvae and certain annelids.

III. Excretion. Activities associated with excretion.

IV. Protective behavior (Fig. 5). Protection from
    adverse influences. Adverse influences are repre-
    sented by predators, competitors for food or terri-
    tory or shelter, temperatures that are sufficiently
    high or low enough to be harmful, light in some

instances, and concentrations of moisture that vary
from the normal sufficiently to influence activity.
Also, in aquatic habitats, salts, minerals, and hy-
drogen and hydroxyl ions may be of such a con-
centration as to be detrimental, and they may cause
definite types of behavior that result in protection
from detrimental conditions. Those mechanisms
which can serve to protect organisms only from
biotic influences are marked with an asterisk.

A. Self protection.
   *1. Concealment.
      a. Quiescence on appropriate backgrounds—
         often as a result of complete or partial
         tonic immobility—in coöperation with
         camouflage (Warden et al. 1935-40). Erro-
         neously called lethisimulation when the re-
         sult is concealment (IV, A, 3, h).
      b. Camouflage.
         (1) Passive camouflage (by evolving pro-
             tective resemblance to surroundings).
             Protectiveness of apparent resemblance
             to environment must be supported by
             sound evidence for each species. There
             is much evidence to indicate that many
             species of animals are protected from
             predators by their color and form
             (Cott 1940, Pearse 1939).
             (a) Protective color.
             (b) Transparency as illustrated by
                 many plankton organisms. This
                 category may be considered a sep-
                 arate one: IV, A, 1, f.
             (c) Protective shape or form.
             (d) Protective stable color and stable
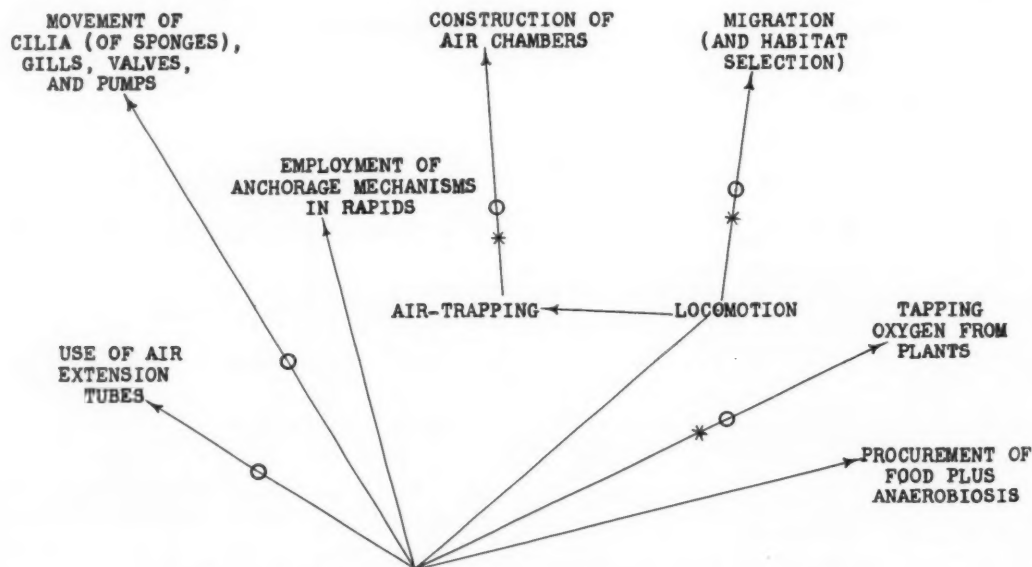   form when they occur together

FIG. 4. Respiratory behavior. Locomotion involved*. Anchorage involved°.

(protective behavior belongs to the next category). Resemblance to dung, etc.

(2) Active camouflage. Passive camouflage often occurs with active camouflage, especially for category (c).

(a) Through chromatophoral activity; occurs for some fishes, crustaceans, cephalopods, chameleons, etc. (Parker 1932, Hanström 1940).

(b) Through placement of natural objects on the body as occurs for spider crabs (Pearse 1939). This is not usually intelligent behavior as at least some crabs do not need a brain to perform their camouflage activities (Minkiewicz, cf., Holmes 1911). This type of behavior is analogous to concealment brought about through excavation (IV, A, 2, b and Fig. 7).

(c) Background selection; occurs for crayfishes (Brown 1939).

(d) Imitation of the environment through behavior of the whole animal as occurs for larvae of geometrid moths (Jordan & Kellogg 1922; Cott 1940).

c. Timing of activity and rest. Timing of community activity to the nychthemeral or seasonal period in which the majority of possible predators cannot see efficiently. Also, timing of rest and shelter procurement to the period when shelters are not used by competitors (Elton 1935).

d. Procurement of shelters, especially those which completely conceal inhabitants; may involve construction of shelters.

e. Minute size. The smallest organisms such as bacteria are not eaten by animals that depend upon sight for locating food and cannot be captured by organisms larger than protozoa and rotifers since strainers and all other traps except current traps are not fine enough to catch them.

2. Removal from adverse influences. Escape.

a. Retreat. (1) Migration (locomotion) to new habitats in which an adverse influence is less pronounced or lacking and (2) movements that lead a portion of an organism away from a detrimental influence. Such movements may occur as negative re-responses to harmful stimuli (Pearse 1939, p. 138). They often occur as either positive or negative responses to either harmless or harmful factors that are always
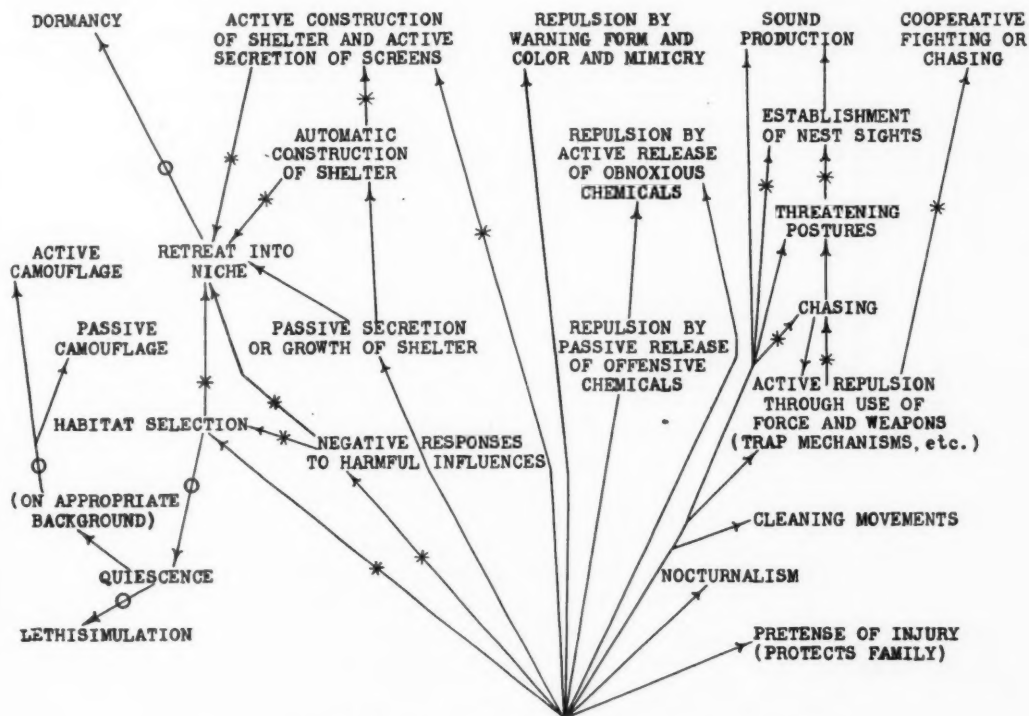

Fig. 5. Protective behavior. Locomotion involved*. Anchorage involved°.

associated with the detrimental influences.
Escape from detrimental influences may
rely upon random movement or upon trial
and error orientation. Response to stimuli
is not always essential for escape to be
accomplished.

b. Obstruction of adverse influences by bar-
   riers.
   (1) Procurement of barriers to adverse in-
       fluences (Fig. 7). The building of city
       and state walls by ancient peoples and
       remaining in niches, especially those
       too small for enemies to enter, belong
       in this category. Active construction
       of shelters may be involved.
   (2) Direct blocking of detrimental factors.
       (a) Active placement of shields as
           when the latter are moved so as to
           receive attacks; occurs for stags.
       (b) Exposure of defense structures to a
           maximum extent. This type of be-
           havior occurs for porcupines, some
           armadillos, and certain sensitive
           plants.
   (3) Blocking openings; dependent upon
       procurement of shelter.
       (a) Active blocking of openings as
           through the employment of heads
           as plugs; occurs for the ants of the
           genus Camponotus (Mann 1935).
       (b) Blocking of openings dependent
           upon retreat; illustrated by snails
           that use operculae or epiphragms.

(4) Coöperative blocking. This mechanism
    is illustrated by animal groups when
    members form aggregates, each unit of
    which plays a part in sheltering the
    group from cold, wind, or predators,
    etc. Musk oxen employ this mechanism
    as protection against predators and
    cold (Clements & Shelford 1939). The
    same mechanism assists in the protec-
    tion of bees from low temperatures.

c. Retreat into or behind obstructions such as
   shelters.
d₁. Timing of activity and rest. Timing of
   community activity to the nychthemeral or
   seasonal period in which the majority of
   possible predators are least active or to the
   time at which temperature, moisture, or
   other environmental conditions are most
   satisfactory (Elton 1935, Pearse 1939, Park
   1939, 1940).
d₂. Dormancy following procurement of shel-
   ter (Shelford 1929, Pearse 1939, Warden
   et al. 1935-40, Benedict 1938).

3. Repulsion of adverse influence.
   *a. Release of repulsive chemicals (odors);
      occurs for Papilio (Comstock 1930).
   *b. Exposure of warning coloration or/and
      form, sometimes in connection with storage
      of distasteful or poisonous chemicals
      (Pearse 1939); includes resemblance to
      faeces.
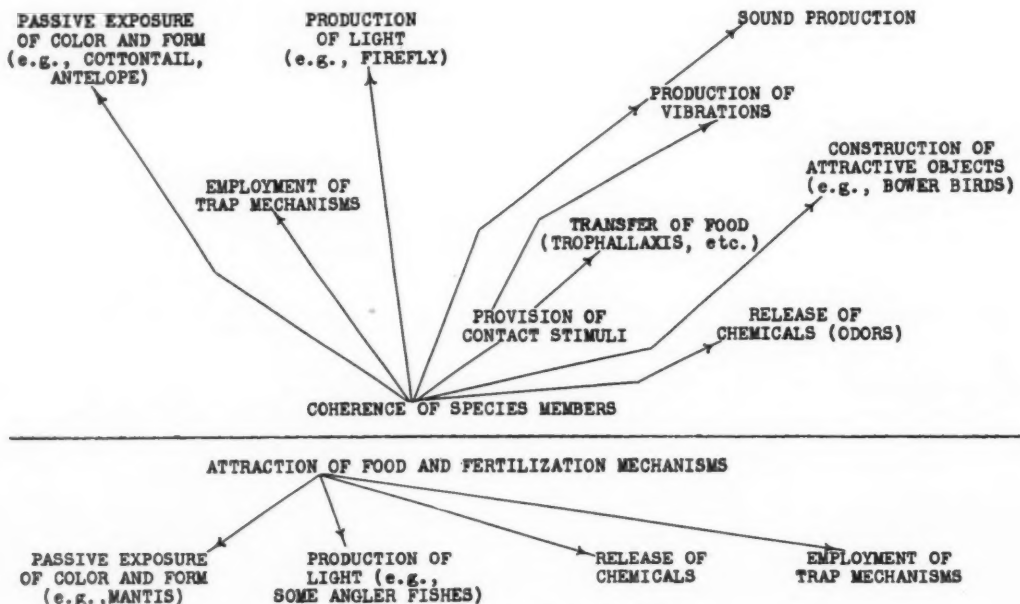   *c. Combination of a and b; occurs for
      Papilio (Comstock 1930).

FIG. 6. Attraction mechanisms.

*d. Mimicry of distasteful species (Pearse 1939, Punnett 1915).

*e. Production of warning sounds or "songs" (Gadow 1908, Kendeigh 1941).

*f. Chasing enemies (Kendeigh 1941). Co-operation may be involved.

*g. Fighting enemies and use of trap mechanisms by direct force (Kendeigh 1941). Co-operation may be involved.

*h. Aggressive attitudes and pretense of aggressiveness (Kendeigh 1941). Consider the aggressive attitude of pus moth caterpillars.

*i. Lethisimulation may in some instances result in the indifference of possible predators that feed only upon living organisms (Holmes 1908, Warden *et al.* 1935-40).

4. Removal or destruction of adverse influence.
   a. As a consequence of bathing and combing (Pearse 1939, p. 323).
   *b. Killing or incapacitation of intruders through the use of trap mechanisms (Fig. 3).

5. Counteraction of adverse influence. Some animals such as bees may counteract low temperatures by remaining hyperactive. High temperature may be counteracted by humans through increasing rate of evaporation as by fanning.

B. Family, commensal, and species protection. Protection of offspring, potential offspring (eggs), mate, or members of a colony.

1. Concealment.
   a. Quiescence on an appropriate background in conjunction with camouflage while the body covers or encloses offspring or any members of an organismal unit (see IV).
   b. Nocturnalism when behavior of some members determines the time of activity or location of other members of an organismal unit.
   c. Procurement of shelters when safety of immature is effected.

2. Escape.
   a. Movement away from adverse influences when family members are carried within or on the body or when members follow or imitate a leader that moves into a more suitable environment.
   b. Category IX is often a protective mechanism when members of an organismal unit are carried, or when members follow or imitate a leader that moves into an environment in which adverse influences are less effective.
   c₁. Removal of organisms (or potential organisms) out of reach of predators at least in regard to other individuals of the same
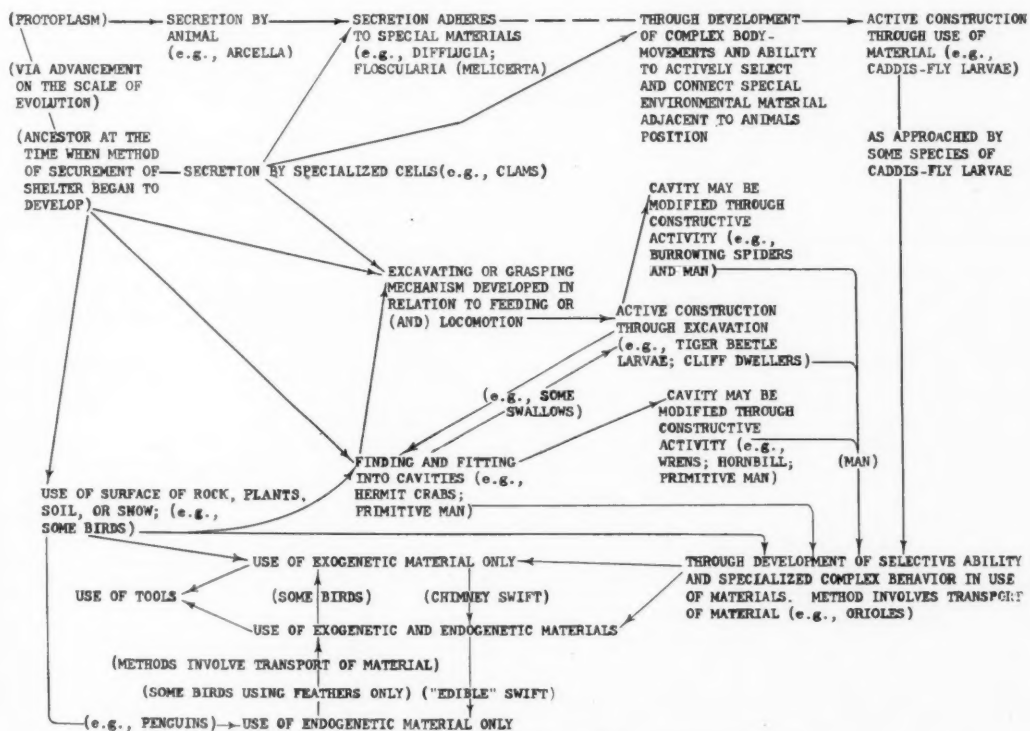

FIG. 7. Evolution of activities involved in procurement of shelters.

species. This mechanism occurs for lace-wings and certain snails which form eggs that are situated upon long stalks.

c₂. Remaining in niches or retreating into niches when members are carried by or attracted to a leader. This applies especially to instances in which shelters are too small for enemies to enter. Secretion or construction of shelter may be involved.

d. Timing of activity to the nychthemeral or seasonal period in which the majority of possible predators are least active, or to the time at which temperature, or moisture, or other conditions are not suitable. This aspect of behavior protects family or group members when the latter are carried by or led by special individuals (Elton 1935).

e. Rapid reproduction. Reproductive rate may be sufficiently high to permit a portion of individuals to outnumber the total number of adverse influences. This applies to all species that have not become extinct, and once held for extinct species up to the time of their extinction. This provision applies especially to those species that lack most of the other protective mechanisms; for example, most grasses, some plankton organisms, many insects, and bacteria. Reproduction is essentially a mechanism that prevents the complete destruction of protoplasm.

3. Repulsion (IV, A, 3, points a, b, c, d, e, f, g, h).

4. Removal or destruction of adverse influence (IV, A, 4, point b).

5. Distraction of enemies as by self display.
   a. Rapid movement; often occurs in conjunction with point b for many birds.
   b. Sound production such as the singing of male birds.
   c. Simulation of injury (Tomkins 1942).

6. Counteraction of adverse influences (IV, A, 5).

C. Protection of home, territory, and miscellaneous property.
   1. Repulsion (IV, A, 3).
   2. Removal or destruction of adverse influence (IV, A, 4). The most indirect trap mechanism is the propagation and release of parasites of crop pests.

V. Cleansing behavior.

A. Body cleaning movements: scratching, bathing, preening, and combing.

B. Elimination of refuse from abodes. For example, elimination of feces from nests.
   1. Independent elimination of refuse as occurs for young herons.
   2. Dependent elimination as occurs for the immature of most passerine birds. Parents remove egested material for a period after the young hatch (Kendeigh 1941).
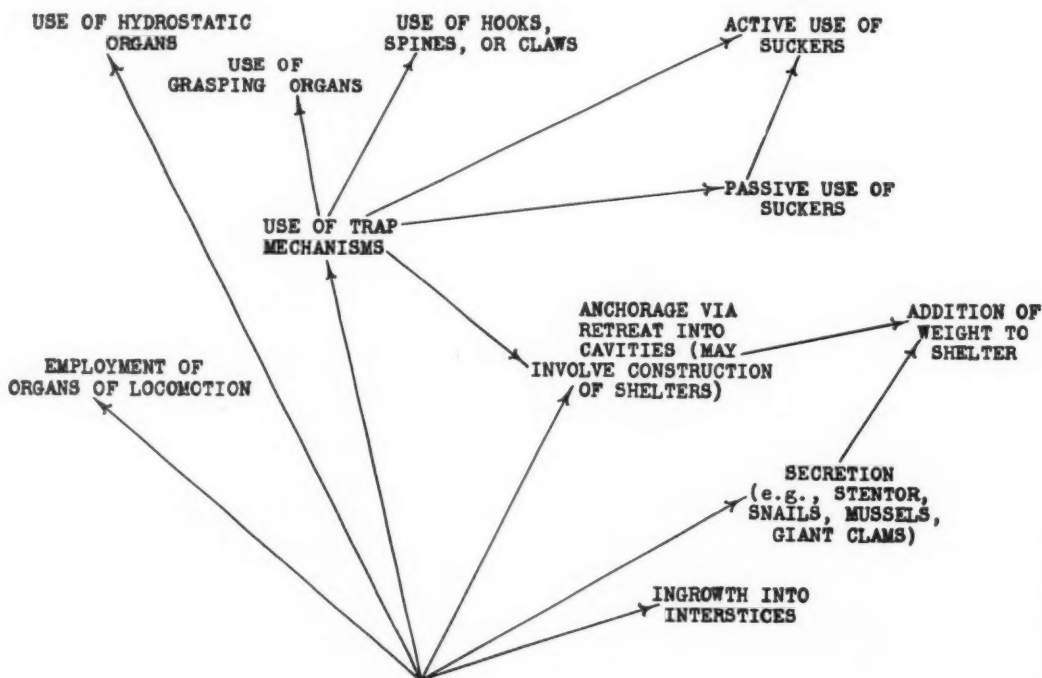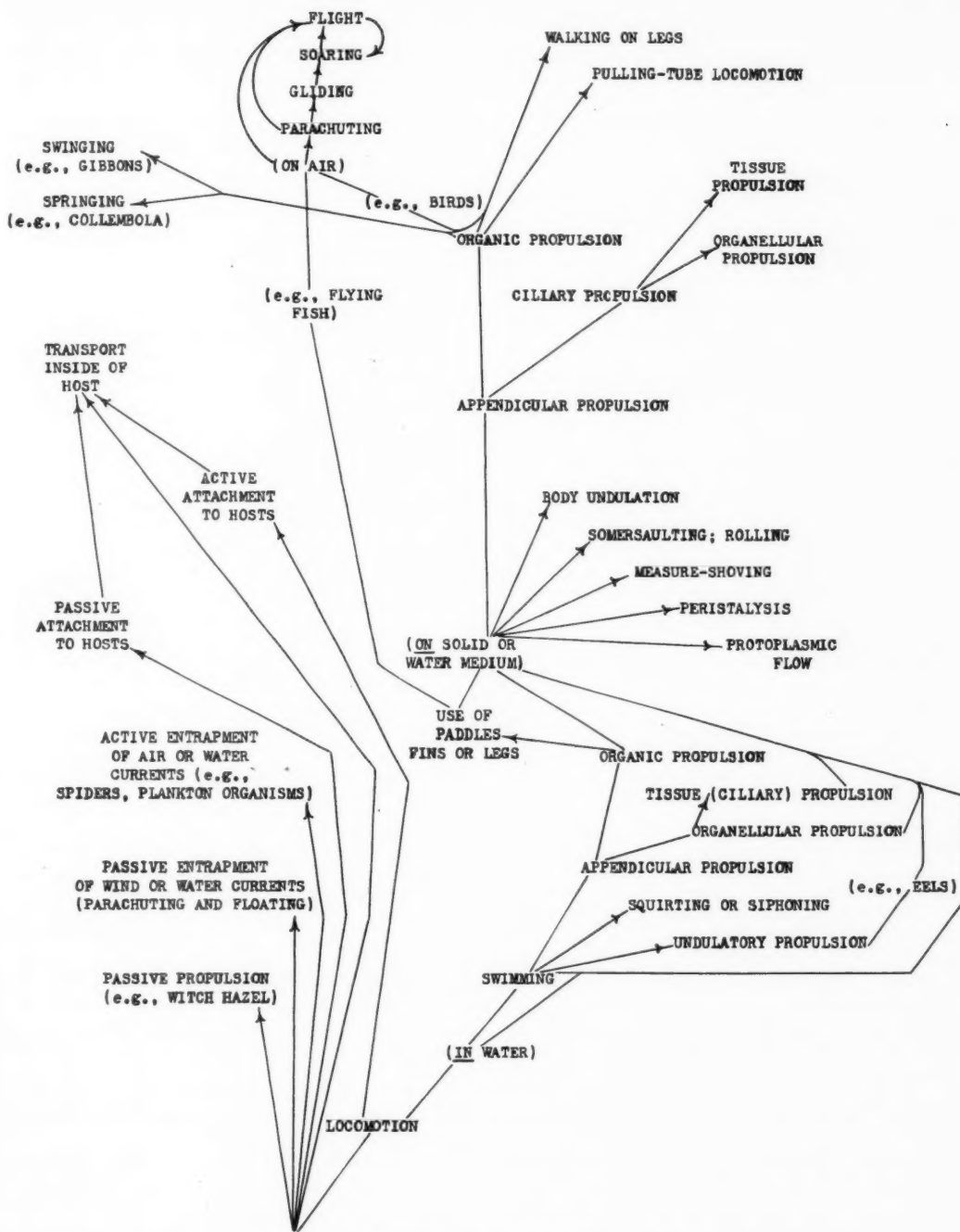

Fig. 8. Anchorage mechanisms.

FIG. 9. Evolution of transportation mechanisms.

VI. Organizational behavior; for example, combing as occurs for fur bearers and arranging objets of the habitat in order as occurs for bees and ants (Wheeler 1910, Comstock 1930).

VII. Reproductive behavior (Warden *et al.* 1936-40, Pearse 1939).

A. Migration or/and habitat selection as illustrated by eels and salmon (Hammerton 1930, Powers 1941).

B. Defense of nest and territory (Kendeigh 1941, Nice 1941, Howard 1920).

C. Courting. Use of sound organs (Kendeigh 1941, Warden *et al.* 1940, p. 764).

D₁. Construction of shelter.

D₂. Employment of anchorage mechanisms.

E. Employment of coherence mechanisms such as (1) release of sex or species odor-producing chemicals, (2) display of color and form, (3) production of sound, (4) production of contact stimuli, and (5) production of light (Fig. 6).

F₁. Budding and mating plus oviposition or birth.

F₂. Budding plus oviposition or birth.

F₃. Fission.

G. Care of eggs, mate, and/or young (Warden *et al.* 1936-40, p. 769-770). This category may be subdivided according to nutritive, respiratory, and protective functions, etc., covered by activities under I, II, III, IV, V (and perhaps VI to some extent), and [1], p. 18.

VIII. Restful activities.

A. Sleep and sleep movements (Shelford 1937, p. 31, Park 1940).

B. Hibernation (including aestivation) (Shelford 1929, Pearse 1939, Benedict 1938, Morgan 1939). May involve the formation of hibernaculae either for individuals or for species protoplasm; occurs for Hydra, Volvox, some squirrels, etc. (Borradaile 1923, p. 248).

IX. Elimination of irritation, pain, discomfort, or displeasure caused by influences not detrimental to a significant extent. Influences and adaptations may be the same as those listed for protective behavior (IV). Positive responses to stimuli either assist in the performance of some life function (I-V or VI inclusive), lessen pain or discomfort (IX), give pleasure (XI), or are blind (XIII).

X. Prerequisite activities. Behavior prerequisite to any life function; for example, learning a trade or working at an occupation. Humans usually carry out prerequisite activities when penalties or motives such as rewards are realized. Some organisms carry out prerequisite acts by working for humans, by providing food or entertainment, or by serving as symbionts to other species.

XI. Recreation and behavior that gives immediate pleasure as occurs for some birds, otters, and many primates. For example, otters repeatedly slide down banks that border bodies of water (Hammerton 1930).

XII. Complex activities. Some activities serve simultaneously as complexes of more than one life function. Five subdivisions are given. Many more are possible.

A. Protective-cleansing-organizational behavior. Combing is not necessarily confined to categories V, VII, or VIII. This act may simultaneously serve an organism as a means of organization of external conditions, cleansing, and protection.

B. Nutritive-protective behavior. Some migrations probably protect certain animals from adverse climatic conditions and at the same time bring about availability of food.

C. An activity may be both restful and recreational.

D. Nutritive-respiratory behavior. Migration in a stream may bring about satisfaction of both nutritive and respiratory requirements.

E. Nutritive-protective-respiratory behavior.

XIII. Blind activities. Some activities cannot be explained as a function of any adaptation. Some activities do not always appear to be related to purposes or definite needs.

A. Some migrations; for example, as occur for insects (Williams 1930).

B. Some hibernations. The factor which brings about hibernation of the beetle, *Cicindela hirticollis* Say, is not yet explained (Shelford 1929, p. 154). This hibernation finally is accompanied by winter and is then adaptive. Hibernation of this beetle is blind only up to the time that an adverse environment exists.

C. Some abnormal actions (Part K).

D. Some tropistic behavior; for example, as for nocturnal animals attracted to artificial lights.

The adaptive functions of particular structures and their actions must be determined with considerable care. Trichocysts are commonly regarded as a mechanism that tends to protect Paramecium from the attacks of Didinium. The following procedure demonstrates that trichocysts probably have no protective value to Paramecium. The cover slip and mounting medium are removed from a micro-slide preparation of Paramecium individuals in various stages of being eaten by Didinium. A stain for exploded trichocysts is added and the material remounted. Usually no evidence of the presence of a single expanded trichocyst appears for any of the stages of engulfment. Use of a special staining technique is ordinarily not necessary for making trichocysts visible, but evidence is more reliable when special methods are employed.

A method of fixing Paramecium in these stages is used by well-known dealers in biological supplies and rarely—if ever—causes expansion of trichocysts; so, a prepared slide affords the evidence mentioned as well as would observations of living material, providing it were possible to see expanded trichocysts on normal living specimens.

POSSIBLE ASPECTS AND SUBCLASSIFICATIONS OF THE PRINCIPAL ECOLOGICAL ACTIVITIES

In those instances in which references are not mentioned in connection with behavior traits, consult such general treatises as have been presented by Shelford (1929), Pearse (1939), Warden *et al.* (1936-40), Heilbrunn (1937), and texts on taxonomic groups such as those concerned with entomology. In those instances in which hypotheses or theories have been drawn from any sources, citations to authors are given.

Physiological Ecology may be studied according to several standpoints. The most important of these aspects are: vital physiological activities, classes of complexity of action, responses, guiding mechanisms, orientation, adaptations, adjustment, timing of activities, relative importance of endogenous and environmental factors that govern activities, modification of behavior, physiological functions of aggregations, and abnormal behavior.

Autecology merges with both physiology and synecology. Behavior may be studied according to the following standpoints (points 1 through 9 have autecological applications; synecology is covered by points 3 through 11):

1. Physiological activities (see physiological ecology above).
2. Adjustment in behavior.
3. Modification of behavior.
4. Timing activities: ecological causes and results.
5. Place relationship between organisms and their environment.
6. Importance of activity to survival of organismal units: community, species, colony, symbiotic or commensal unit, individual.
7. Nature of biotic food and shelter relationships.
8. Extent that organisms are exposed in communities.
9. Methods employed that influence other individuals.
10. Activities may affect physical or biotic environments, or both.
11. Extent of influence upon environment.

[1] PHYSIOLOGICAL ACTIVITIES

PART A. VITAL PHYSIOLOGICAL ACTIVITIES

Div. 1. Vital individualistic activities.
I. Nutritive activities.
II. Respiratory activities.
III. Excretion.
IV. Secretion: secretion of protective mucus (Planaria); secretion of shelters (clams, octopuses), etc. (see VIII).
V. Growth and differentiation; that is, embryonic and postembryonic growth and differentiation, metamorphosis—including pupal differentiation (Weiss 1939, Hanström 1940); regeneration (Loeb 1924).
VI. Rest. Recovery from fatigue.

VII. Rejuvenation. Conjugation and fission may be of immediate vital importance for some organisms such as certain species of infusoria.
VIII. Protective activities: autonomy, regeneration, secretion of mucus and shelters, secretion of poisonous or obnoxious chemicals, fighting of disease as by development of antitoxins or antivenins, counteraction of endosmosis by employment of contractile vacuoles, etc.

Div. 2. Vital species activities. Besides the physiological activities that are of immediate vital importance to individuals, the following are important for the survival of species.
I. Reproduction.
A. Asexual reproduction for some species. Fission; or, budding followed by oviposition or birth for parthenogenetic species.
B. Sexual reproduction. Budding and mating followed by oviposition or birth; or budding plus external fertilization.
II. Care of embryo or immature.
A. Automatic provision of nutrition to embryos or immature in some species; occurs for Peripatus, guppies, Gambusia, dog-fish sharks, mammals—especially placentals and marsupials.
B. Protection of immature. Protection is provided by mammals, especially placentals and marsupials, Cladocera, Peripatus, guppies, Belostomatidae, skates through provision of egg cases.
C. Provision of oxygen to immature. Automatic physiological provision occurs for placental mammals, guppies, and Peripatus. Provision through dynamic behavior occurs for crayfishes by means of oscillation of pleopods.
D. Provision of an excretory outlet for immature; occurs for placental mammals, guppies, Peripatus, etc.

Div. 3. Vital group activities. Besides the physiological activities covered in Division 1, several are especially important for continued existence of groups.

Most activities involved in aggregations may be too complex to be considered within the scope of physiological ecology. On the other hand, individuals may be regarded as organs in the aggregation and all of their activities regarded as physiological. Cooperative and peck-order activities are often essential to the existence of groups where a high degree of organization is required (Allee 1931, 1938). Physiological activities that are vital to the existence of aggregates especially for sessile forms include reproduction. Tropistic reactions of many individuals to a common source of stimulation are sometimes responsible for the formation of groups (Allee 1931).

Div. 4. Vital community activities. Communities may be regarded as super-organisms (cf., Allee 1931, p. 352, Clements & Shelford 1939, p. 22). Species are equivalent to organs, and individuals are comparable to cells. Members of commu-

nities must interact in a definite manner if superorganisms are to survive. The following activities must occur in superorganisms.

 I. Species procurement of food. The amount of food secured must be in small proportion to that which exists, or must be obtained through effort and expenditure of considerable time. Securement of food by a species must not be overly successful (Clements & Shelford 1939, p. 185), but must be sufficient to provide for an increase in reproduction at times. Kind of food accepted may change at times (Shelford 1937, p. 31) and tends to depend mostly upon what is available.

 II. Provision of enemies. Communities must provide at least one predator or parasite for each species (Clements & Shelford 1939, p. 185), except for those species which have a low coefficient of reproduction (due either to adverse physical conditions of the habitat or to low reproductive capacity) and for those species which have special difficulty in finding or obtaining food. Eagles and parasites or hyperparasites do not require enemies to check their abundance. Enemies may change from time to time (Shelford 1937, p. 31).

 III. Provision of shelter. In some communities such as tundras, hot dry deserts, and some grasslands, plants do not provide shelter to many of the larger community members, and burrows constructed by one species serve as habitations for one or more different species. In forests, only a small proportion of species depends upon the inanimate environment for shelter, and the direct provision of shelter is an important activity of plant constituents. It is important that this activity of plants be maintained if the existence of certain types of communities is to continue.

 IV. Retreat. For example, nocturnal associations must retreat during the day by way of some method of concealment to prevent their being destroyed by diurnal associations (Elton 1935). Diurnal time-associations are concealed by darkness at night from nocturnal time-associations. Time-association is substituted here for time-community as used by Elton.

PART B. CLASSES OF COMPLEXITY OF ACTION

Div. 1. Extent to which control of activity is direct or indirect. Activities differ in complexity according to whether they are carried out directly through protoplasmic action or executed by remote control through function of a nervous system, through influence of substances carried in circulatory systems, or through functions of both nervous and hormonal mechanisms. The behavior of various chromatophores illustrates these stages of complexity (Parker 1932, Hanström 1940).

Div. 2. Extent to which behavior is instinctive, learned, modified by intelligence, or innovated (Parts I and J also, pp. 368-375).

I. Simple instinct. Elementary instinct.
 A. Spontaneous protoplasmic activity.
 B. Direct protoplasmic response as for Amoeba and some chromatophores (Holmes 1911, Parker 1932).
 C. Guidance of activity by organelles; for example, function of the stigma in many flagellates, and neuromotor regulation of activity in many protozoans.
 D. Spontaneous protoplasmic activity of tissues and organs (such as effectors) of metazoa; for instance, repeated waves of ciliary movements on ciliated epithelium responsible for locomotion of Planaria, activity of certain glands such as the secretion of shelter by clams, and action of special muscles such as the beating of myogenic hearts.
 E. Direct protoplasmic response to external stimuli in specialized cells of metazoa; neuroid and neuromuscular activity (Parker 1919).
 F_1. Wave response; as when a wave of muscular contraction occurs on the margin of the bell of a medusa, or a wave of ciliary movement occurs on a unicellular or multicellular base.
 F_2. Continuous wave response; as when the completion of one wave cycle stimulates the origin of a new wave stimulus; probably occurs for the beating of cilia on Vorticella.
 G. Response to rhythmic release of spontaneous nervous impulses that originate in ganglia (Prosser 1934); illustrated by the beating of neurogenic hearts and the movements of entomostacran phyllopods (direct observation).
 H. Reflex action (Pavlov 1927, cf., Warden et al. 1936; 1941); activity dependent upon unmodified, spontaneous, nervous activation of effectors as results through stimulation of sensory receptors located on the organs that are finally activated. Afferent and efferent nervous paths run parallel to each other for most of their course and an original sensory impulse is reflected by an adjustor. Reflex and reflection are derived from the same Latin root. Reflex is a misnomer for deflected action. If it is preferable to retain the term reflex to cover deflected action, then two types of reflexes must be recognized according to two separate classes of complexity: (1) simple reflex or reflected action (point H), (2) deflected action (the next point).

I. Deflection.
 1. Direct shunting. Shunting or abridged deflection. In this category, a nervous impulse is switched directly from the point of stimulation to another part of an organism.
  a. Mirror shunting. An impulse is shunted to the opposite side of an organism.
  b. Orthometameric or axial shunting. Internuncial adjustors switch nervous impulses to adjacent areas along the body axis.

2. Central deflection or central transfer of nervous action; central deflection. Activity results through stimulation of sensory receptors located on organs other than those that are activated. Afferent and efferent nervous paths do not run exactly parallel to each other. Original sensory impulses are deflected by a central adjustor, the brain. This type of mechanism was presented by Loeb (1918) to explain certain tropisms of arthropods. Loeb did not attempt to explain how tropisms may be modified in accordance with conscious localization of stimuli in mental space, desires, volition, and intelligence. The fact that specific characteristics of tropistic behavior may be inhibited or modified following tropistic experience does not indicate that explanations originally presented by Loeb to account for orientation of adult arthropods should necessarily be incorrect. The ability of many animals to regulate behavior so as to accomplish original tendencies after one side is injured indicates that psychological phenomena of an order higher than at first realized often occur in many organisms (Warden et al. 1940, p. 63, 781, 783). It is not unreasonable that one of these psychological phenomena that assists in controlling behavior in many lower as well as in higher organisms amounts to desire in some instances. Experimental evidences show that deflection mechanisms account at least in part for the original nature of tropistic action for the arthropods studied by Loeb (1918), that is, for the tropistic tendencies previous to their modification. Abridged and central deflection also account for many compensatory movements (Holmes 1911, p. 39), although some compensatory movements involved in equilibrium of higher organisms result through proprioceptive reflex action. Deflected nervous action is responsible in part for many individualistic activities, to include scratch movements and body cleaning movements when foreign substances or irritations on the body provide the stimulation for movements.

II. Compound instinct.

  A. Chronological instinctual behavior. Consecutive occurrence of specific and different unlearned, un-innovated actions. In compound instinct, completion of one act serves as a stimulus or release of a new tendency that starts another type of specific action. To start an act serves as sufficient stimulation for executing it. Successive activities depend upon a chain of stimuli, most links of which are brought about by an animal's own activity.

    1. Spontaneous centrogenative compound instinct. Stimuli from the external environment are not involved. Native activity of whole organisms is dependent upon spontaneous activity of a controlling nervous center that may in some instances be regulated by hormones; for example, body cleaning routines as occurs for flies, crayfish, mice, etc., and singing of birds independently of environmental stimulation. Descriptions of cleaning movements of some invertebrates have been presented by Szymanski (1918).

    2. Envirogenative compound instinct. An environmental stimulus starts a chain of stimuli no longer dependent upon stimuli produced by external conditions. A male canary may be prompted to sing by the presence of a female and may complete the song after the removal of the female.

    3. Externally guided compound instinct. External stimuli and responses are involved at more than one stage of action, for example as occurs for birds during nest making.

      A single step of a complex instinct is equivalent to a simple instinct. The first step in execution of a fighting instinct is approach towards an enemy. A chase may ensue and end without further involvement of instinct. If an enemy does not leave when approached by an aggressor, further steps of fighting instinct tend to take place (Herrick 1905).

  B. Reversal of instinctive action. For example, first experiences in homing as when gradients or landmarks are present to guide activity. Carrying out reversal of instinctive action is not dependent upon previous experience of going through the process. The activity process is not learned nor innovated, so it must be classified as instinctive. Memory of features in an environment are required in some instances as for homing behavior of some higher animals. Abstract memory is not always involved as illustrated by the homing behavior of chitons and limpets (Crozier 1921, cf., Warden et al. 1940; Holmes 1911, p. 187, 188).

III. Learned action. Conditioned action. (Kinsey 1941.)

  A. Direct training. Actions are conditioned by experiences that create associations between actions or between abstractions, or between abstractions and action. The tendency for associations to occur through experience and the tendency for action to be conditioned by associations are instinctive. Conditioned actions are learned.

    Conditioned deflected action. Activity is dependent upon conditioned nervous associations that are not immediately modifiable. (Conditioned deflection is usually known as conditioned reflex action. *Reflexes* are nor-

mally executed by instinct and do not lend themselves to conditioning.)

Habits are action or thought chains that are created by associative experience. Links in chains may be composed of actions, thoughts followed by specific actions, actions followed by specific thoughts, or may occur between thoughts only. Some mental habits are coincident with, some precede, some follow, and others are independent of bodily activity.

Habits that have a primitive physiological basis do not differ essentially from conditioned deflected action mechanisms. Habits that depend upon conscious centers differ from conditioned deflected actions, since habits that depend upon conscious centers are immediately modifiable at least in humans.

B. Transfer of training (may belong under IV, cf., psychol. texts).

IV. Intelligent action. Activity may be modified intelligently through learning, or through reasoning and forethought (innovation, point V). Learning may occur by trial and error, by what is directly observed, or by way of ideas received through communication. Points of advantage gained through learning are: (1) characteristics of efficient action, (2) method of action, (3) what acts lead to success or a goal regarded by individuals as desirable, (4) what acts lead to pain and what ones lead to agreeableness. Activity may be modified intelligently as follows:

A. Modification through guidance of activity of organs (e.g., as organs of locomotion) in accordance with whether objects or acts symbolize pain or satisfaction, that is, according to conditioned mental state.

B. Modification through increased efficiency in action as is attained by reduction of intermediate and unnecessary movements (or thoughts) originally involved in complex activities; that is, by elimination of random movements.

C. Modification through guidance of a nerve center so as to carry out an original tendency or a desire when one method or mechanism is blocked by injury or removal. Such an instance of modification occurs for robber flies in their reaction to light after one eye is painted (Loeb 1918). Refer to modifiability of activity in Part J, p. 370. Ability to modify behavior is not evidence that an original, natural reaction to a stimulus is not instinctive.

D. Modification through invention (point V below). Behavior may be modified intelligently by addition of new features or elimination of certain aspects originally involved.

V. Innovation. Creative activity. Originality in Action (Morgan 1933).

A. Originality involved in choice of action. Originality may be involved when choice must be made between actions, all of which symbolize pain, or all of which symbolize satisfaction. Choice of activities followed by human beings is determined by relative importance of desires. Most human desires are based upon relative importance of the following (point 1 illustrates primitive desires). The following are usually purely instinctive or absent in most species.

1. Physiological desires: tendencies to eat, sleep, etc. Selection of food, mate, habitat, time of rest are in part guided by originality and individual differences in taste.

2. Selfishness, desires to be happy, to acquire wealth, to have social approval, to dominate others, to be praised.

3. Desire to satisfy emotions built upon wishful thinking.

4. Desire to do or repeat creative work that appeals to aesthetic sense. Activities that give rise to art, music, poetry, etc.

5. Desire to help others to relieve suffering or to increase happiness.

6. Desire to discover and know what is true and to guide one's activities in accordance with facts, a basis for invention and research.

7. Desire for high quality of action or product of action. Points 4, 5, 6, and 7 are peaks in the evolution of behavior.

B. Development of new methods by substitution of new acts that modify or tend to satisfy natural tendencies when instincts cannot be carried out naturally. This explanation usually accounts for an animal's adoption of young that belong to remotely related species.

C. Purely creative activity. Creative activities depend upon mental trial and error processes and constructive imagination that depends upon nervous associations and symbols. Creative activity is involved in the arts, inventing, metaphysics, etc.

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Sympathy, curiosity to discover and know what is true, and determination to discover and do what is best for the welfare of all concerned are among highest mental achievements.

Comments

Evidences that innovations occur as an outcome of mental ingenuity for animals besides primates are not common (Holmes 1911, p. 164-259).

However, mutations that bring about improvement in adaptiveness of behavior are analogous and perhaps equivalent to innovations. It is possible that when such mutations first occur in single individuals, behavior traits that follow have the appearance of representing innovated behavior. It becomes a question of whether a tendency to carry out a definite type of behavior or whether an ability to make a

suitable invention (adjustment) is inherited. Observers tend to consider behavior instinctive when it characterizes all individuals of a species if individuals are capable of showing such behavior when isolated following birth. If beneficial behavior is shown by a small portion of individuals of a species, the tendency is to consider such behavior as an expression of intelligence. It is perhaps not possible in all instances to determine whether behavior is innovated by individual intelligence. This is a difficult problem to solve for the wasp, Ammophila, which has been observed to use a pebble as a hammer (Peckham & Peckham 1905). The possibility exists that certain tropical bats did not construct shelters for themselves until recently. This trait was recently discovered in several widely separated localities (Barbour 1932, Chapman 1932, cf., Allen 1939, p. 68-69). If bat leaf shelters existed previous to recent years, they must have been overlooked by the many zoölogists now famous for their descriptions of the tropics, and this seems unlikely. Beneficial behavior may be originating in some species at present. This should not seem strange as there must be a first occurrence for every trait, and evolution has not come to an end. It is of great interest to know whether beneficial behavior traits arise in the offspring of one pair of parents and become numerous only as these characteristics appear in their descendents. The construction of shelters by bats suggests that behavior traits may arise independently at about the same time in many individuals.

Desires, volitions, and manner of thinking may depend upon random mental activity in combination with automatic or predetermined mental processes entirely guided according to influences of past and present experiences in turn dependent upon quality and quantity of inherited equipment and environmental opportunities. Loeb (1918) held such a view.

PART C. RESPONSES

(Morgan 1891-1930, Loeb 1893a, 1900-24, Jennings 1906, 1910, Pearse 1906-39, Holmes 1907-16, Mast 1911-18, Shelford 1911-30, Holmes 1916, Allee 1926, cf., 1931.) Responses may differ in the following respects:

I. Intensity or magnitude of action (Shelford 1937, p. 28, Bayliss 1931). Extremes of influence are (1) cessation of activity, (2) initiation of activity.

II. Rate of action (Shelford 1937, p. 28). Extremes of influence are (1) cessation of activity, (2) initiation of activity.

III. Action may be carried out by direct protoplasmic response; or may be executed through function of a nervous or humoral mechanism, or by a mechanism involving both nervous and secretory influences (Parker 1932, Hanström 1940) (see complexity of response, Part B).

IV. Type of stimulus that excites response (Part D), and kind of sense that responds to stimulus: photic response, color response (Pearse 1911, Brown 1934), thermic response, pain response (Cannon 1915, Boring et al. 1939) pressure response (Shelford 1929), etc.

V. Responses differ according to type of activity that constitutes response: feeding, mating, or fighting, etc., may constitute the response of an animal as it sees another individual (Shelford 1937, p. 28).

VI. Extent to which response is positive or negative or indifferent to stimuli received including objects perceived (Shelford 1937, p. 28). This category includes orientation responses, but also applies to refusal or acceptance of food, etc.

VII. Speed at which reaction follows stimulation; that is, length of reaction time and latent period (Bayliss 1931).

VIII. Miscellaneous adjustments (point [2]).

IX. Responses differ according to position and nature of stimuli (see factors that may account for variations in research results, p. 173, and Warden et al. 1940, p. 63, 780-783).

PART D. GUIDING AND REGULATING
MECHANISMS

Physiological — including psychological — mechanisms that guide or control behavior. These mechanisms serve to guide activities of whole organisms. Some of them guide the behavior of single cells and tissues during embryonic development and differentiation (Weiss 1939). Guiding mechanisms may serve for orientation and taxis that lead towards securement of food, mate, and habitat. They may restrict organisms by trap action to areas that lack particular influences and may cause animals to retreat from adverse influences.

Recognition, selection, and rejection of food, mate, and habitat, and of materials put to various uses such as construction of shelter depend upon guidance mechanisms. Guiding mechanisms may be responsible for the nature of reactions (see Responses, Part C).

I. Behavior guided by single mechanisms.

  A. Activities guided by fundamental physiological non-psychoprojective mechanisms.

    1. Photoresponse.

      a. Photo intensity response (or "photoreaction") pertains to reaction of organisms to light, and is not concerned with responses to visual images. Response occurs to presence or absence of a light stimulus or varies according to the intensity of light.

        (1) Direct photoresponse: immediate reaction brought about through sensitivity of organisms to light. Special photoreceptors are not always necessary, for example, as for Amoeba. On the other hand, organs sensitive to light may be highly complex.

        (2) Indirect photoresponse: reaction of gonads of fishes, birds, and mammals to changes in photoperiodism; re-

action of some chromatophores to hormonal regulators released according to influence of illumination (Amer. Med. Assoc. 1935, p. 271, Hanström 1940).

b. Photo wave-length response; occurs for organisms that may or may not form mental concepts of colors, yet react differently to widely different wave-lengths.

2. Chemo-reaction. This reaction involves those activities controlled by way of a simple chemical sense, gustatory sense, or olfactory sense (Imms 1937, Powers 1941).

3. Gravity-reaction. Centrifugal force reaction.
a. Ortho-gravity reaction: negative reaction to gravity leads some kinds of caterpillars to food (Loeb 1918). See magnetic response. The force of gravity is reproduceable by centrifugal force, although the pull of objects towards the earth is not due to centrifugal force.

b. Diagravity or lateral gravity reaction (diageotropism) as shown by twining plants (Rober 1929, Stiles 1936).

4. Thigmoreaction. For example, withdrawal reaction of shell-bearing mollusks when touched by moving objects. Thigmoreactions guide some organisms in selection of habitats (Shelford 1914).

5. Push-reaction. Unilateral pressure reaction. For example, some reactions to current: rheotropism.

6. Baro-reaction. This type of response is dependent upon sensitivity to total pressure. For instance, regulation of volume of air in swim bladders of many fishes.

7. Thermoreaction. Temperature may serve as an exogenous stimulus when animals come into contact with objects or media capable of causing sensations of hot or cold. This is possible only when nerve endings that are sensitive to heat or cold are present in the skin. Temperature sensations can occur only when temperatures with which organisms come into contact are different from body temperature. Ordinarily, temperature exerts its influence upon metabolic rates as an endogenous influence, especially for poikilotherms, but also for homeotherms. That is, environmental temperature often exerts its influence by changing inner body temperatures. The result is due to an internal temperature state, and not to a stimulus. Direct responses to sensation of heat or cold may be designated exothermal responses and the result in this instance is due to the reception of stimuli that continually originate from the external environment. Changes in behavior that result from modification of internal temperatures

may be referred to as endothermal results or endogenous thermal responses. Thermoreactions are treated by many authors (e.g., Shelford 1929, p. 22, 373-375).

8. Hydroreaction. Response may be due to a sensation of touching water, so a thigmoreaction may be involved. Response to water may be dependent upon water temperature or to temperature changes brought about by presence of water. Increased humidity reduces evaporation and thus slows reduction in temperature. Decrease in humidity has the opposite effect. Contact with water or selection of special concentrations of humidity may be governed by the manner that contact with water can modify osmotic relations, turgidity, and water content of skins. It is probable that hydroresponses, humidity responses, and osmotic pressure reactions are interrelated in some instances. Hydroreactions may be coupled with temperature or touch sensations and may act as a single stimulus in rare instances if at all. Hydroreaction and humidity-reaction are listed separately from other influences for convenience and completeness in organization of material. See Allee 1926, cf., 1931. Refer to II, p. 41.

9. Evaporation reaction (Shelford 1913, 1914a, cf., 1929). See II, p. 41.

10. Osmotic pressure reaction and turgidity reaction. When hands are in contact with soap water for a long time, an "osmotic sensation" is produced. The emptying of contractile vacuoles in protozoa serves to counteract osmotic influx of water. That this process occurs as a response to presence of vacuoles is proved by disappearance of vacuoles when a marine water medium gradually replaces fresh water. Many cells tend to take up water and salt until a high concentration is reached. Finally certain changes (reactions) occur which alter the endosmotic process. A similar phenomenon occurs when cells excrete or secrete surplus amounts of substances required for their own existence (Livingston 1903, p. 140, Krogh 1939).

11. Vibration reaction. Occurs for trap-door spiders (Passmore 1935, p. 229).

12. Muscle-tension reaction. Proprioceptor reflexes are employed in mammalian balance, especially when sight (IB, 1, a) and semicircular canals are eliminated from action (IIC, 2).

13. Magnetic response. Galvanoresponse (Loeb 1918, Warner et al. 1935-40, Stetson 1937). Response to gravity has no dependence upon sensitivity to magnetic waves ("magnetism"). It has not been proved that organisms encounter electric currents in

natural habitats nor that they respond to magnetic waves.

B. Behavior guided by single psychoprojection conceptions. Objects and sensations perceived in space are projected in mind through a phenomenon of imagination. Space-perception and perception of feelings, objects, and happenings in space is consciousness when practically coincident with and brought about by actuality. The accuracy that characterizes judgment of distance by mantids, kingbirds, and chameleons as they attack their prey proves that the images seen by these animals occur within protoplasm. The optical images and what happens to these images are re-created in a mental world that represents the world of reality. Consciousness requires no other criterion, assuming that it is correct to rule out the sensation of self-consciousness as unimportant. Self-consciousness is probably not an essential characteristic of consciousness. It is unknown to most young children and is not a continuous mental experience for adults. We do not react directly to the objects which we see. Our responses are to mental concepts of objects which we project into space. When objects and happenings are located practically where they seem to be located, consciousness is being experienced. It is important to regard consciousness as not quite coincident with actuality. Objects under water when viewed from the air are not seen where they are located. The sun is seen only after its light travels for eight minutes, so the sun is usually two degrees further in its course than what it seems to be. At a distance of 1,090 feet, animals hear sounds one second after sound producing vibrations are created. Common perceptions usually occur almost simultaneously with actuality.

1. Reactions based upon sense of distance, spatial localization of objects, and changes that occur in the spatial relationships between objects; that is, reactions to objects conceived in space. A chameleon's capture of a fly illustrates a response that involves a sense of distance and spatial localization of an object. Spatial localization is accomplished by several mental mechanisms, and responses may be classified according to the type of mental phenomenon that serves to create a mental spatial concept.

    a. Vision response. Visual image reaction. The sense of distance and localization of objects reaches greatest perfection through creation of mental space concepts by means of bifocal vision. Perception of depth is probably acquired as organisms learn the significance of shadows, highlights, and angles. Many animals employ "psychoprojection movement" (e.g.,

rapidly turning or swaying the head); occurs for wrens, owls, humming birds, and mantids. Such movements provide images of objects at different angles and afford a basis for judgment of distance similar to that of bifocal vision.

    b. Auditory reaction. Spatial localization of vibrations ("sound").

    c. Odor response.

    d. Taste response.

    e. Touch response.

    f. Psychothermal response. Responses to feeling of heat or cold.

    g. Pain response.

    h. Articular localization response. The sense of position of body parts is dependent upon skin and muscular sensations.

    i. Tickle sensation response.

2. Reaction to symbols. Concepts may symbolize pain, bitter taste, satisfaction, insignificance, unknown significance (concepts that lead to curiosity), etc. These mental concepts are created in mind by way of the senses and nerves which serve as intermediaries between conscious centers and environment. The concepts become symbols through direct experience with objects or through what is learned from other individuals.

3. Reaction to perception of weight. Sense of weight is often a mental concept probably dependent upon the touch, muscular, and pressure senses. Reaction to gravity can be —in part at least—a reaction to an animal's sense of the weight of its own body parts.

4. Reaction to perception of proportion. Many animals including humans rely upon their recognition of characteristic body proportions in reacting positively to members of their species and negatively to enemies.

5. Reaction to concept of speed (see 6).

6. Reaction to concepts of time and space-time; occurs when used by predators as they attack rapidly moving prey. Kingfishers can capture a moving fish by striking where the fish will be. This involves attempting to strike ahead of the actual location of prey. Humans use this sense in estimating distance they have traveled during a definite period of time, and it is possible—but not likely—that some migrating animals also rely upon this criterion of distance traveled. This is possible only when a concept of speed of travel is also present.

7. Optic sense; taking advantage of any principle of optics. Kingfishers, gulls, terns, and certain other birds strike accurately at objects under water regardless of the fact that—due to diffraction of light as the latter passes from one medium into another of different density—objects under water are

not where they appear to be at most angles of observation above water.

8. Responses to ultra-abstract concepts; that is, to concepts of right and wrong, truth, beauty, theory of relativity, etc. Such highly abstract concepts guide human social behavior and the planning of research, etc.

II. Behavior guided by compound response mechanisms.

A. Compound complementary physiological reactions. Psychoprojection is not involved.

1. Osmothermic evaporation reaction. It is not conceivable that evaporation exerts any influence by its process alone. Evaporation may modify temperature and can bring about a decrease in water content of cells such as those which form skins.

2. Thigmopressure reaction. Touch and pressure stimuli probably act together in some instances.

3. Hydroreactions are usually as complex as evaporation reactions. Reaction to contact with water may involve temperature, pressure, osmotic, and chemical reception in any combination.

B. Compound supplementary reactions. Psychoprojection may be involved. Response occurs to one type of stimulus but is conditioned by one or more stimuli of other kinds than the one which excites a definite type of response (p. 173-177).

1. Chemically conditioned photoreaction (Welsh 1930).

2. Photo-thermic reaction. Tendency for reaction to light may be reversed or eradicated by temperatures above or below certain limits.

3. Gravity-pressure reaction. Tendency for reaction to gravity may be reversed or eliminated by total pressures above or below certain limits.

4. Gravity-nutritive reaction. Change in nutritive state may reverse or destroy tendency to respond to gravity.

5. Gravity-thermic reaction. Temperatures above and below specific limits can cause reversal or extirpation of tendency to react to gravity.

C. Physiological psychoprojection mechanisms. Psychoprojection is involved in one or more of the aspects that constitute a reaction.

1. Unilateral pressure visual response. Rheovisual response. The orientation of many fishes in streams is controlled partly by their direct response to current and in part through apparent movement of that which is seen. Objects that are seen do not necessarily form very definite mental images, but are probably projected into space in imagination. That is to say, the photic aspect of response of fish to objects in the environment belongs on the psychological

level (Lyon 1904-09, cf., Loeb 1918, Shelford 1929).

2. Muscular-gravity-visual response. Mammalian balance and locomotion normally involve proprioceptive reflexes, deflected actions dependent upon stimulations that originate in semicircular canals and response to images.

D. Compound psychoprojection mechanisms. Most or all of the perceptions that are responsible for a reaction are psychoprojections.

1. Visual-muscular or visual-skin sensation reactions. This type of complex is involved in recognizing localizations of body parts, surface pains, etc.

2. Visual-sound reaction. When objects are heard and seen simultaneously, they create a more concrete concept than when only one sense is stimulated. Addition of stimulation to sense of color adds further to the vividness of mental concepts. The popularity of sound and color motion pictures compared to that of the silent cinema illustrates this point.

3. Osmothermic evaporation reaction when psychoprojection is involved. It is not unlikely that evaporation may exert influence in part through thigmosensitivity, so osmothermic thigmoreactions probably occur. Probably an osmothermic thigmosensation occurs when one's hands are withdrawn from strong soap water.

4. Miscellaneous. Vision may act along with the olfactory sense to produce sensations and reactions. The olfactory and gustatory senses sometimes act as a complex. Skin sensations may consist of the simultaneous perception of more than one type of stimulus; for example, psychothermal thigmoresponse, touch thermal pain response, etc.

III. Stimulus production reaction mechanisms. Behavior of an animal is brought about by simultaneous response to stimuli created through its own activity.

A. Vibration-production audioreaction complex. This mechanism is employed by bats in locating objects in path of flight (Griffin & Galambos 1940, Galambos & Griffin 1940). Blind persons can learn to rely upon the same mechanism by producing sounds in walking or by tapping a cane instead of through employment of the voice.

B. Light-production visual-reaction complex. This mechanism is employed by some deep sea animals that produce light (Harvey 1940).

C. Chemical release-reaction complex as occurs for limpets.

PART E.　ORIENTATION

Besides fitting into the following classifications some orientations can be classified according to Parts A, B, C, D, F, G, H, and/or I.

Div. 1. Manner in which organisms orient to stimuli as determined by result of response. Tropisms and orientation plus locomotion (Loeb 1918, Meyer & Anderson 1939, Wigglesworth, 1939).

I. Kineses: (A) ortho-, and (B) klino- (Fraenkel & Gunn 1940).

II. Taxes: (A) klino-, (B) tropo-, and (C) telo-.

III. Transverse orientations: (A) compass reaction; for example, light-compass reaction, (B) dorsal or ventral reactions to stimuli.

Div. 2. Method of accomplishing orientation.

I. Random movement or/and trial and error (Jennings 1904-10, cf., Child 1924).

II. Spiral movements; employed by homing pigeons, wasps, and bees (Holmes 1911, p. 194, Stetson 1937). The function of spiral movements has been supposed to afford opportunity of observation for wasps (Peckham 1895). A different possibility is suggested for homing pigeons (Stetson 1937).

A spiral path in a horizontal plane should eventually lead to home territory. However, it has not been demonstrated that any animals employ this method throughout unknown territory as a method of homing. Such a method is probably not used by organisms that have been carefully studied. Homing pigeons spiral when released in territory unknown to them, then straighten their path and tend to fly a fairly definite course towards home in practically all instances (Stetson 1935). Orientation tests for homing tendency should be judged by the direction in which animals start out on their courses when released and not by determining the proportion of animals that are successful in reaching home.

III. Guidance of orientation by special stimuli (Parts C and D).

A. Unconditioned orientation.

1. Instinctive reaction to objects.

2. Instinctive reaction to environmental factor gradients.

3. Imitation of that which is immediately observed. Includes following of leaders in migrations.

B. Conditioned orientation.

1. Learned reaction to "landmarks." Landmarks may be represented by objects that create images or light-shadow impressions, vibrations that produce recognizable sounds, particular temperature levels or chemicals that produce recognizable odors, etc. Landmarks may be learned through previous experience or through what is conveyed abstractly by way of communication.

2. Learned reaction to gradients. Such reactions depend upon associations learned by experience or communication.

3. Physiological memory. Muscular memory (Pieron 1913, cf., Pearse 1939).

IV. Complicated methods.

A. Intelligent action may be involved (e.g., invention, construction, and/or employment of compasses or other special instruments).

B. Complex of other methods.

V. Unexplained methods of orientation. It is difficult to believe that landmarks serve to guide orientation for many species of bats, especially in long migrations. Some migration routes of bats follow those taken by certain species of birds (Griffin 1940, Hitchcock 1940).

The orientation mechanism of homing pigeons and many other species of birds is not known (Fraenkel & Gunn 1940). Landmarks and conscious memory do not often play a part in migrations (Peterson 1941, p. 55).

Homers are trained to return to their nests by releasing them only short distances from their homes at first and gradually increasing the distance between known territory and point of releasement (Lea 1923). Probably training homing pigeons is accomplished by increasing their tendency to return home through ruling out distractions at first, thereby causing them to increase their sensitivity to whatever factors serve to guide them.

It is important to recognize the significance of a number of facts that concern the homing ability of pigeons. (1) For the total of known records in which homing pigeons have been released over 1,000 miles from their homes, the proportion of returns is high within a number of days following their release. Some return flights have covered as much as 2,100, 2,200, and 7,200 miles (Vance 1937). No visible "landmark" except the sun could have served as a directional guide in these instances, and returning home by reliance upon random and trial and error movement should require a number of years on the average. Therefore, repeated or independent returns over new and lengthy courses must be ruled as not results of chance inasmuch as there are no failures on record to counterbalance the successes. (2) Pigeons that have acquired the ability to reach home when released 100 miles from their stations may immediately be released at distances of 500 miles with about 100 percent success (Lea 1923, p. 9, 11). In such an instance, the gap of territory with which the birds are not acquainted amounts to about 300 miles with an allowance for a vision range of 100 miles. Under such conditions, there is no opportunity for recognition of landmarks upon release. (3) Homers almost invariably start out in their homeward direction (Stetson 1935, 1937). It is this characteristic that should serve as the principal basis for judgment of the accuracy of orientation. Flight in a straight course may be preceded by a brief narrow spiral. (4) Pigeons reach their destinations when released in smoke and fog (Lea 1923). (5) Homing pi-

geons are trained to be independent. There is no evidence that some homers follow leaders. Rather, the evidence is to the contrary (Lea 1923, p. 8). (6) Evidence has been obtained from several sources that pigeons may be sensitive to magnetic or other electrical waves (Stetson 1935, 1937, Vanee 1937, Pop. Mech. 1937). In reference to orientation of homing pigeons subjected to radio frequency waves, it is held that experimenters so far have usually failed in method of control to make results convincing (Stetson 1937 and personal communication 1940). Stetson's theory may explain a mechanism of orientation that would not require use of a special sense organ or complex of organs for permitting detection of direction (Stetson 1935, 1937). Stetson's suggestion is that sense of direction may depend upon electrical stimulation of central nervous systems by way of nerve cords. If this mechanism is functional, magnets placed over the heads of the birds would not prevent electrical reception. (7) Views of the ground from the air are not required. An injured pigeon with clipped wings has been known to walk its last stretch home (Vanee 1937). (8) As flight ranges are increased from one to 500 miles, etc., birds make better records when they are always carried in the same direction for release (Lea 1923). This indicates that pigeons probably learn to respond to some type of gradient. (9) Pigeons make a high proportion of returns when released at places that require their following radically different directions than those previously taken (Pop. Mech. 1935, 1940). This suggests that whatever stimulus serves as a directional guide is of general distribution. Pigeons can fly both with and against winds (Lea 1923), so the possibility is slight in most instances that odors serve as important guides. (10) Pigeons have been recorded in several instances to fly a number of miles out of straight courses in going around storms (Pop. Mech. 1935, Vanee 1937). This fact does not support the idea that birds rely upon definite courses characterized by visible landmarks. (11) It is recognized that pigeons rely upon vision in finding their home lofts after the latter are practically reached. However, reliance upon recognition of visible objects in the territory that surrounds lofts can never be important since homing pigeons do not wander far from home (Lea 1923). Pigeons that are released far from mobile stations, the locations of which are set within twenty-four hours previous to their release, have no time to learn landmarks in surrounding territory (Pop. Mech. 1935, 1940). Lofts have been moved from New Jersey to Ohio with successful results. (12) Rupture of semicircular canals is reported to destroy homing ability without destruction of ability to fly (Hannah 1929, Vanee 1937). In the Northern hemisphere, water moves counter-clockwise as

it leaves a funnel. It moves in a clockwise direction in the Southern hemisphere. Perhaps this is due to the fact that the water particles towards the equator move around the earth's axis at a more rapid rate than do those towards the nearest pole. Since water in a small funnel is sensitive to direction of earth movement, it should not seem strange if some animals can sense direction of earth movement with the aid of semicircular canals. (13) The following information applies to night flying pigeons. (a) The best records which amount to nearly sixty miles have been made on the darkest nights when moonlight is absent (Hannah 1929, Pop. Mech. 1940). Some of these have occurred after 11:00 P.M. during rains (Pop. Mech. 1940). (b) Nocturnal flights of 20 to 60 miles are as successful over the ocean as over land (Pop. Mech. 1935, 1940). (c) Speeds average higher for night flying than for day flying. (d) Homers reach dark lofts and illuminated lofts in about the same amounts of time (Pop. Mech. 1940). (14) It appears that valleys and coasts are followed as a result of other advantages than the presence of landmarks (Hannah 1929). (15) Application of homing data to statistical analysis (page 53) indicates that chance and landmarks taken together do not account for percentage of homing returns.

It is not unlikely that some organisms may be assisted in orientation by general or specific "odors" liberated by different communities, biomes, soil types, seas, or lakes. Some animals are not sensitive to specific chemicals to which others are sensitive (Imms 1937). This point may be demonstrated for individuals of a single species as well as for those of different species. Some persons are not capable of tasting phenyl thiourea (Sturtevant & Beadle 1939, p. 43). It is significant that certain chemicals may not serve to stimulate sense organs of some animals—either as a result of their specific constituency or due to their weakness of concentration—and yet be capable of stimulating sense organs of other individuals or species. Sex chemicals of some female lepidoptera are barely noticeable if noticeable at all to human beings. Males of each species are highly sensitive to the chemical released by females of their species. Males of some species are stimulated by these diluted chemicals over distances of several miles (Rau & Rau 1929, Poulton 1929). Chemicals of plant hosts stimulate female lepidoptera at great distances, though human beings may or may not be able to detect any plant odor. If an odor is noticeable to humans, it remains to be demonstrated that the chemical responsible for stimulation of the human olfactory sense is the same one to which other animals respond.

Mechanisms involved in finding of water by toads and certain mammals have not been demonstrated. Some turtles are said to employ geo-

tropism in locating water (Loeser 1940). This mechanism may serve the same purpose for a few other animals.

How organisms orient excavations so that tunnels of nests meet at particular points is not known. Consider the difficulty involved in explaining how moles and kangaroo rats construct nests without trial and error attempts to make ends meet that would result in the existence of many blind alleys (Borradaile 1923, p. 93, Clements & Shelford 1939, p. 81).

Trial and error, chance, environmental guidance, and memory of landmarks have not been shown by experiments to explain the mechanisms by which some organisms orient their movements.

The performance of physiological experiments will be necessary to demonstrate what mechanisms animals employ to accomplish orientation. To attempt to solve this problem for homing pigeons, olfactory nerves of many birds must be cut, and a portion of those released must wear glasses that prevent ordinary vision.

Div. 3. Probability that accident accounts for homing. Probably, for homing pigeons and bats that have not had opportunity to learn landmarks over large areas, the chance ratio that accident could account for return is approximately equal

to: $1 : \dfrac{2\pi D}{\widehat{xy}}$ (Fig. 10).
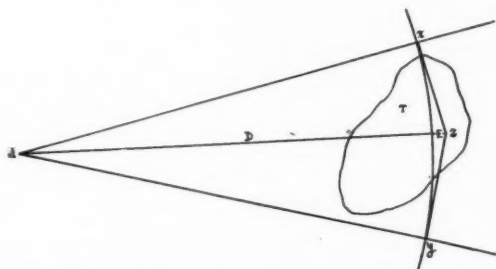
FIG. 10. Probability that chance accounts for homing of animals that tend to locomote in a straight line through regions unknown to them

$$= 1 : \frac{2\pi D}{\widehat{xy}} \text{ or } = 1 : \frac{360°}{\angle xdy} \text{ or } = \frac{2 \sin}{360}.$$

When d equals the point at which an animal is released outside of territory with which it is acquainted; dx and dy are lines that extend from d to the outermost limits of the home range; dx and dy should be drawn outside of the limits of the home range to an extent that represents the distance the animal can see landmarks for the height at which locomotion occurs. The figure is drawn to scale so the addition of the proper distance is not difficult. $D + E =$ the hypotenuse of the triangles. $D =$ the radius of a circle that has its center at d. It is a bisector of angle xdy. $\widehat{xy} =$ an arc formed by angle xdy as it intercepts the circle. The formula may also be expressed as follows:

Chance of accidental return $\Big\} = 1 : \dfrac{360°}{\angle xdz} \text{ or } = 2 \dfrac{(\text{angle value of sin})}{360°}$

This formula applies as it stands to the homing of pigeons. Corrections need to be applied to the formula for migrations of species that follow bodies of water when the latter serve as visible landmarks and to those species that do not tend to fly in straight lines. The formula cannot be applied to any species that may tend to fly in a spiral or at random over unknown territory.

Div. 4. Mechanisms that accomplish orientation.

I. Orientation by growth, or change in tissue tension (e.g., some plants and Bryozoa). Regulation of water content of cells and growth can control orientation movements (Borgström 1939, Stiles 1936). "Growth" often amounts to absorption of water by protoplasm.

II. Orientation by dynamic movement of organisms or specialized parts of organisms.

    A. Orientation accomplished through protoplasmic response (e.g., Amoeba).

    B. Orientation accomplished through employment of organs or organelles that push or pull directly against environment.

        1. Accomplishment by parts of single cells or tissues (e.g., ciliates, Planaria).

        2. Accomplishment by body movements (e.g., Hydra, snails, snakes).

        3. Accomplishment through appropriate use of specialized locomotor organs as occurs for some echinoderms, many marine worms, arthropods, cephalopods, and most chordates.

PART F. ADAPTATIONS

(Dublin 1903, Osborn 1903, Shimer 1903, Lull 1904, Robertson 1906-24.) Environmental influences can alter structure and physiological processes (Turresson 1922, Hall 1932, Müntzing 1935, Turrill 1935, Duggar 1936, Clausen et al. 1939, Galdston 1940, Hiesey 1940, Castiglioni 1941, Dobzhansky 1941). Behavior may be indirectly modified. Structures and physiological mechanisms are commonly regarded as determined by heredity. However, environmental influences are responsible for bringing about development or holding in check those developmental and differentiation mechanisms which are inherited. Particular conditions of environment can be responsible for both development and degeneration of mentality, eyes, etc., and can bring about both strengthening or atrophy of muscles and other organs. These facts have nothing to do with the inheritance of changes that occur in parents as a result of environmental influences (Lamarckianism). These facts do explain why it is not possible in some instances for named genotypes, species, and subspecies types to be recognized as actualities. Many taxonomic problems remain unsettled unless it can be shown whether differences that appear to distinguish species or subspecies are due to inherited peculiarities or to the

results of environmental influences (Div. 2 and
Uvarov 1928).

Div. 1. Adaptations in behavior of protoplasm
and physiological mechanisms. Complex struc-
tures of organisms are not inherited as such.
Mutations modify structural development by
modifying behavioristic tendencies of protoplasm
via changes in the structure of genes. Modi-
fication of the dynamic behavior of protoplasm
finally leads to a variety of structural adapta-
tions (Weiss 1939). Finally, the nature of
dynamic behavior of whole organisms is precon-
ditioned by the nature of the structures of which
it consists. The physico-chemical basis of be-
havior is explained by a number of writings
(Goldschmidt 1923, 1938, 1940, Newman 1937,
Coghill 1929, Davis 1936, Estabrooks 1936, Gray
1937, Hill & Clegg, 1937, Lit. Dig. 1937a, Sci.
News Letter 1938-41, Shoemaker 1939, Brain
1940, Kaempffert 1940, Kinsey 1941, Clark 1941,
Gibbs 1941, Stockard 1941).

Adaptations to an environmental influence may
be structural and not involve dynamic movement.
An example of such an adaptation is offered by
the shells of snails. However, no structural
adaptations can come about except through activ-
ity and expenditure of energy. Behavior adapta-
tions cannot be regarded as isolated entities. On
the contrary, behavioristic adaptations must be
considered in combination with both external
and internal structures upon which they depend.
Adaptations consist of structures with their asso-
ciated physiological equipment and activities per-
formed. Some adaptations apply to factors of
limited distribution*. Others apply to factors of
general distribution. The latter are the more
primitive.

I. Adaptations for procurement of food.
    A. Feeding mechanisms.
        1. Separator mechanisms such as osmotic
          contact apparatus including plant roots;
          also, plankton strainers of whales and gill
          rakers of fishes. Excavation may be in-
          volved as for Sacculina and other para-
          sites.
        2. Trap mechanisms; include suspension
          feeding apparatus (current traps) pos-
          sessed by Bryozoa, rotifers, and such
          ciliates as Stentor; *other types of traps
          such as grasping traps, etc.
    B. Locomotor mechanisms.
    C. Anchorage mechanisms.
    D. Attraction (adherence) mechanisms.
II. Adaptations for respiration.
    A. Respiratory surfaces (lungs, gills, trachea,
        etc.), usually associated with devices for
        moving them or associated with pumps and
        valves for moving air or water to and away
        from such surfaces or anaerobiosis. *Spe-
        cial tubes or reservoirs may be employed for
        leading air to respiratory surfaces.

    *B. Locomotor mechanisms of aquatic air breath-
        ing animals (Fig. 9).
    *C. Anchorage mechanisms of aquatic air breath-
        ing animals (Fig. 8).
III. Adaptations for excretion. One of the most
    important excretory traits is the behavior in-
    volved in keeping abodes and general habitats
    clean. This problem is solved by caterpillars
    through combination of excretory behavior with
    egestion. Dung pellets composed in part of
    excretory material roll and drop away and in
    so doing remove the possibility of excrement
    being eaten or induction of putrefaction in
    food.
IV. Adaptations for protection. (1) Secretion of
    epidermis, shells, mucus, plates, webs, inks.
    (2) Trap mechanisms such as chelicerae of
    starfish, etc. (3) Chromatophores and pig-
    ments or absence of pigments. (4) Timing
    mechanisms. (5) Locomotor mechanisms. (6)
    Reflex and deflection mechanisms. (7) Mecha-
    nisms for dormancy; temporary return of ho-
    meotherms to a poikilothermal condition. (8)
    Release of chemicals. (9) Sound production.
    (10) Tonic immobility. (11) Cleaning mech-
    anism such as combs (Pearse 1939, p. 323,
    Hegner 1932, p. 285). (12) Reproduction. If
    all existing life were never destroyed by nat-
    ural death and other causes, reproduction
    would be a disadvantage instead of an advan-
    tage.
V. Adaptations for reproduction.
    A. For fertilization.
        1. Without sperm transfer. Locomotion of
          males may be involved (points b and c).
          The motility of spermatozoa is important.
          a. Retention of eggs until after fertiliza-
             tion, although sperm may be released
             independently of the presence of fe-
             males and fertilization may be external
             or internal; occurs for some medusae
             and hydroids such as Hydra.
          b. Release of eggs and sperm independ-
             ently or in close consecutive order; in-
             volves production of many gametes.
             Occurs for some fishes such as cod.
          c. Release of eggs and sperm simulta-
             neously during "mating" or amplexus;
             occurs for some fishes and amphibians.
        *2. Dependent upon sperm transfer.
          a. Adaptations for procurement of and at-
             tachment to females.
             (1) Locomotion.
             (2) Anchorage mechanisms such as fore-
                leg suckers of Dytiscus (Comstock
                1930, p. 482).
          b. Adaptations for sperm transfer. Sperm
             transfer apparatus is treated by Borra-
             daile (1923, p. 161, 170). It may be
             intromittent or extramittent. Peculiar
             methods are employed by cephalopods,

leeches, spiders, and it is believed the Chimaeridae fishes may employ a frontal clasper.

B. For release of immature or potential young (eggs). Apertures are usually present but are lacking in rediae and certain other organisms including certain Diptera larvae in which paedogenesis occurs.

1. Haphazard release of new generation in combination with reproduction of many individuals.

2. Placement of new generation in niches or on special food; may involve use of ovipositors and sense of larval food as occurs for ichneumon flies (Comstock 1930, p. 917).

3. Care of immature. (1) Provision of food may involve employment of placentae and mammary glands. Trap mechanisms for food securement, locomotion for food procurement, and anchorage during food transfer are usually involved. Anchorage may be provided by oviducts or such pouches as those possessed by Daphnia and marsupials. (2) Provision of oxygen, (3) excretion, and (4) protection have been presented sufficiently to form a framework for further detail (see [1]).

VI. Adaptations that assist in retention or procurement of habitat and shelter. (1) Streamlined form (Needham & Needham 1935), (2) lateral or dorso-ventral compression of growth, (3) anchorage mechanisms including locomotion, hydrostatic organs, secretion, spines, and trap mechanisms, etc., and (4) secretion, locomotion, and trap mechanisms in connection with construction of shelters; ability to use tools possessed by humans and tailor ants, etc.

VII. Adaptations for dispersal (see [5], Part B).

A. Passive mechanisms.

1. Current or energy trapping.

a. Mechanisms for wind transport.

(1) Minute size.

(2) Development of wind catching mechanisms.

(a) Passively secured; for example, many seeds.

(b) Actively secured; for example, spiders (Fabre, cf., Kinsey 1938).

b. Mechanisms for water transport. Incorporation of air pockets; for example, cocoanut, statoblasts of Pectinatella.

2. Attachment mechanisms.

a. Use of anchorage mechanisms; occurs for many seeds, statoblasts of Pectinatella, glochidia.

b. Living within organisms; occurs in many instances of parisitism and commensalism.

3. Propulsion mechanisms; for example, jewel weed, witch hazel, etc.

B. Active mechanisms. Locomotion (Fig. 9), that is, locomotor organs with related equipment.

VIII. Regulatory mechanisms. Mechanisms employed in regulation of rate of metabolism, water content, water reserve, osmotic pressure and permeability, freezing point, enzymes and antibody formation, respiration, neutrality of blood and tissues, temperature (Shelford 1929, Heilbrunn 1937, Dill 1938, Pearse 1939, Krogh 1939, 1941, etc.).

IX. Specialization for sensitivity, reaction, and adjustment to the various environmental factors such as light, pressure, salts, enemies, etc. (Heilbrunn 1937, Yapp 1939).

Div. 2. Modification of structure

Growth or Alteration of Vitality With Consequent Modification of Behavior

I. Modification by response to temperature or to temperature plus some other factor such as nutrition (II).

A. Wing pattern phenocopies and pseudocopies result for some species of insects when pupae are subjected to particular temperatures (Goldschmidt 1938). Melanism does not occur in the butterfly, *Papilio glaucus* Linn, north of the United States possibly as a result of temperature influences (Holland 1931, p. 318). There is a relation between amount of pigment, amount of heat absorbed, and consequent intensity of movement (Uvarov 1928).

B. Exposure to low temperatures during development may cause reduction in size of appendages (Doms 1916, Sumner 1915, cf., Weiss 1939) and of course influence the nature of eventual dynamic behavior.

C. It appears that exposure to low temperatures causes some reduction in size of adult lepidoptera through temperature influence during pupal differentiation (Holland 1931, Goldschmidt 1938, Roberts 1942). There is thus some evidence that Bergmann's phenomenon is at least in part a direct result of environmental influence. There is usually a positive correlation between size and speed of movement. Large individuals of Papilio fly more rapidly than do small ones (direct observations).

D. The color bands on feathers are a result of a rhythmic temperature and metabolic phenomenon under environmental control (Riddle 1908, cf., Shelford 1937). Temperature may influence behavior so as to affect structure which acts again on behavior (Uvarov 1928).

II. Modification by response to nutrition (see XIII also).

A. Reduction of food for caterpillars as might result from early onset of winter can result in

formation of dwarf pupae and development of dwarf imagos for certain butterflies (Holland 1931, p. 318, Roberts 1942a).

B. Many studies have indicated that vitamins, sunlight, and definite minimum quantities of water and food are required for both mental and physical development. Reductions below requirements lead to dwarfism and abnormal shape of body parts. Both rate of growth and type of growth are influenced by nutrition (Borradaile 1923 and texts on nutrition).

C. Kind and amount of food, living space, and other environmental factors indirectly determine morphology and color of certain castes in insects, for example, in bees. Behavior of different castes is radically different (Forel 1928, Emerson 1939, Maeterlinck 1939).

III. Modification via responses to chemical influences. Great modifiability of form and behavior may be dependent upon chemical influences. Consider control of sex in Bonellia, caste and sex control in bees.

IV. Modification through response to light (Blum 1941, Duggar 1936).

A. Illumination is known to be important for utilization of vitamin D which in turn influences size, shape, and strength of certain body parts. Illumination influences the amounts of vitamins A and D in milk production (Chick & Roscoe 1926, cf., Shelford 1929).

B. Light is a regulator of food manufacture—and therefore, a controller of growth in plants.

C. Light brings about development of certain pigmentations (Borradaile 1923, Hesse 1937, p. 532), and lack of illumination may bring about elimination of pigment.

D. Some animals do not develop eyes unless subjected to illumination (Noble 1931, cf., Hesse 1937, p. 533). The development of eyes when light is present in turn results in a different type of behavior for animals that live exposed to illumination than what would occur if eyes were absent.

E. Changes in photoperiodism may cause alteration in structure and behavior (Marcovitch 1923, Shull 1927-29, cf., Chapman 1931).

V. Modification through influence of mating and fertilization. Fertilization can account for behavior and structural differences. For example, consider differences of structure and behavior of queen bees as contrasted to drones. Whether eggs will be diploid or haploid in some instances depends upon whether mating occurs, for example, rotifers and aphids.

VI. Modification by influence of behavior. Behavior may account for structural differences as shown for certain locusts (Uvarov 1928).

Queen ants remove their own wings which in turn makes a type of behavior (flight) impossible.

VII. Modification as a result of aging. Structure and behavior may depend upon changes that accompany aging; this is especially notable in those organisms that experience metamorphosis. This category is of interest especially to taxonomists and ecologists because many organisms are described under two names as a result of dimorphisms that are partly controlled by environmental influences. Among animals that have received two names as a consequence of metagenetic changes are: flukes, tapeworms, some roundworms, polyps, and jelly fishes. The palolo worm divides into two rather unlike parts, each of which were at one time given different species names. In the case of the palolo worm, the time that the epitoke breaks away from the atoke is governed by the state of the moon (Pearse 1939).

This category of behavior and structural changes is important because ecological study is required not only for clarifying the environmental relations of such changes but for ascertaining nature of species.

VIII. Kind of ambient medium. Metamorphosis and consequent type of behavior may depend upon whether the environmental medium is water or air. Consider the axolotl which may or may not retain gills throughout life (Carpenter 1928).

IX. Gregareousness and solitude and change in intensity of action modify morphology and behavior of certain locusts (Uvarov 1928, cf., Allee 1931, Faure 1935, Lea 1938).

X. Osmotic concentration in aquatic environments may alter morphology and as a consequence—behavior (Abonyi 1915, cf., Weiss 1939, p. 140).

XI. Density and viscosity and temperature of aquatic environments may possibly control modification of structure and consequent alteration of behavior. For example, Ceratium, some entromostraca, and rotifers (Wesenberg-Lund 1911, cf., Pearse 1939, p. 67, Carpenter 1928, p. 199).

XII. Nature of selection of mate (coaction) determines kind of offspring. Although this category has a genetic basis, the genetic result depends upon an organism's reaction to environment. Consider the difference in result in pairing of golden and blue-winged warblers to each pairing with its own type. A cross gives a 9:3:3:1 ratio in phenotypes (R. Boulton 1936, personal communication, Nichols 1908).

XIII. Modification by rhythmic growth phenomena as illustrated by tree rings, rings of clam shells, and scales of fishes. In these instances, modification of growth may not have any influence upon behavior. However, the structures listed

are significant as concrete records of behavior and are often records of changes in environmental conditions (Creaser 1926, Hansen 1937, Stallings 1939).

PART G.　ADJUSTMENT

Subclassification may be made according to what environmental factor stimulates physiological or psychological changes. An adjustment is a process of improvement in adaptiveness of an organism to the condition of environment responsible for stimulation of either a physiological or psychological change or both physiological and psychological changes. The abilities and tendencies of organisms to adjust themselves to environmental conditions or environmental changes constitute a class of adaptations. All abilities to adjust or learn adjustment mechanisms are inherited either as a property of cytoplasm or by way of what has been contributed by genes through species heredity. The ability to acquire tendencies or desires to carry out adjustments not already present exists by way of inheritance.

I. Direct adjustment to direct environmental influences.

　A. Physiological adjustment. For example, dogs grow hair more rapidly when taken to colder climates. Physiological changes do not necessarily bring about changes in behavior or psychological state. Psychological adjustment may or may not depend upon physiological adjustment. This category belongs to the field of pure physiology. It also belongs to the field of behavior. In many instances, physiological adjustments may involve movements of whole organisms and may involve response to stimuli provided by the external environment.

　B. Behavior adjustment. Adjustment in behavior for animals low on the evolutionary scale is likely to be dependent upon purely physiological adjustments. Adjustment in behavior for organisms capable of modifying their behavior in accordance with past experience is likely to involve psychological change.

　C. Psychological adjustment. So far as behavior is directly concerned, psychological adjustments may be equivalent to some types of behavior adjustments for those instances in which behavior is definitely related to mental processes.

II. Adjustment to concepts. Self adjustment. Some psychological adjustments such as those involved in recovery from pessimistic philosophies and outlooks are not directly concerned with behavior. All psychological adjustments are dependent upon physiological adjustments inasmuch as mind is a function of a particular kind of substance.

PART H.　TIMING OF ACTIVITIES

Animals and the physiological mechanisms that control their actions may be active continuously or intermittently. Intermittent activity may be rhythmic or arhythmic. Activities may or may not change or synchronize with fluctuations of environmental factors.

It is not suggested that the following outline be used to classify "general activity." The classification may be used for the purpose of classifying specific types of activity: community exposed activity, locomotor activity, securement of food, feeding, mating, or acquirement of shelter. Many physiological activities of organisms fit into this classification in accordance with descriptions given by authors who have treated these subjects. These activities include movements of leaves, petals (Stiles 1936) and chromatophores (Hanström 1940); intestinal movements and "hunger" (Richter 1927, cf., Park 1940); periodic development of gonads (Rowan 1938); migratory tendencies in some birds (cf., Clements & Shelford 1937); nychthemeral migrations for some species of filaria (Elton 1935); periodic conjugation in Paramecium (Sonneborn 1941). References for timing of activities in the day-night cycle: Park 1937; for timing of activities through the year: Shelford 1929, Clements & Shelford 1939; miscellaneous: Craig 1917, Allard 1916-18, cf., Allee 1931.

It is convenient to employ Part I along with timing of activities in this classification. Locomotion serves to illustrate types of activity outlined.

I. Ephemeral activity: pertains to activities that occur but once either for individuals or for particular life stages. For example, mating flights of ants and termites; locomotion of newly hatched meloid beetles (Stiles 1936, Comstock 1930).

II. Continuous activity: pertains to nychthemeral activity and to activity that occurs through seasons and years. This type is illustrated by locomotion of many plankton organisms. "Perennial" activity pertains to activity of animals that do not hibernate or die when subjected to winter or other adverse climatic conditions that recur periodically.

III. Intermittent activity.

　A. Arhythmic activity; may be subclassified according to whether endogenous or environmental factors regulate action. The distribution of activities in accordance with time is also a basis for classification.

　1. Opportune activity. Activity occurs whenever environmental opportunity and physiological conditions permit. Individuals of some species of ants evidently rest from specific activities only when environmental conditions are unsatisfactory for executing them and when fatigue occurs (McCook 1877, Flint 1914, Park, Lockett & Myers 1931, cf., Park 1940). Morning-cloak butterflies and bees are active outside of niches whenever weather permits. Their activities that involve locomotion are arhythmic so far as seasonal time-distribution is con-

cerned, rhythmic so far as most nychthemeral activities are concerned.

2. Occasional or irregular activities. Movements of many reptiles and leeches occur irregularly.

3. Rare activities. For instance, migration of lemmings and migrations of individual birds of some species (Peterson 1940, p. 524). Activities that are regarded as rare for individuals may be regarded as occasional for species.

B. Rhythmic activity.

1. Exogenous rhythm. Environmental rhythm. Environmental rhythms may be subclassified according to the environmental factor or combination of factors responsible for regulation of periodicity. They may also be classified according to whether inhibition or activation are responsible for periodicity.

a. Activation rhythm: a rhythm that occurs when activity increases as a response to rhythmic changes in environmental influences. For example, this phenomenon occurs for the crayfish, *Cambarus virilis* Hagen (Roberts 1936, 1941).

b. Inhibition rhythm: a rhythm that occurs when activity is periodically inhibited by rhythmic changes in environmental influences. For instance: occurs for roaches (Park & Keller 1932) and crayfish (Roberts 1941).

c. Activation-inhibition rhythm: a rhythm controlled in part by inhibitory influence of fluctuating environmental factors and in part by an increase in activity brought about as a response to periodic environmental changes. Locomotion of *Cambarus virilis* fits point c. (Roberts 1936, 1941).

2. Endogenetic rhythm. Endogenous rhythm (Webster 1942).

a. Enviromentally-induced rhythm. Acquired rhythm. Occurs in *Cambarus virilis*.

b. Inherent or innate rhythm (not acquired).

3. Composite rhythm (Roberts 1936): a rhythm of activity, the highest peaks of which depend upon both endogenous and exogenous rhythmic influences to bring about their total normal magnitude.

Some problems that concern nychthemeral rhythms:

Endogenous synchronization of rhythms with occurrence of day and night may be acquired while an endogenous tendency for activity to occur at 24-hour intervals is already present (Roberts 1942).

Averages of activity records of many individuals do not always indicate the true nature of individual activity. In these instances, single activity records reveal more than averages. For instance, individuals kept in constant darkness may retain periodicity in time of occurrence of activity, but peaks of activity may fall at different hours of day and night for different individuals, as results when synchronization of activity with day and night is lost at various rates. The averages of a great number of such rhythmic records shows arhythmicity; that is, a horizontal line when data is represented by a graph covering activity of the 24-hour cycle.

The average interval in occurrence of locomotor activity of the crayfish, *Cambarus virilis*, when kept in constant darkness, is about 24 hours (23.8 hr.) though the intervals between peaks measured to date vary from ten to forty hours. 23.8 hours is the average of forty-three intervals for nine individuals. This indicates that the physiology of the crayfish, *Cambarus virilis*, is probably in accord with a 24-hour plan, even though no fixed endogenetic rhythm is present after animals remain under constant conditions for a few days (Table 1).

The adjectives inherent and innate when applied to endogenous rhythmic tendencies imply that a periodic quality is inherited or inborn (Webster 1942). These terms should not be applied to rhythms unless evidence secured under conditions known to be light-proof indicates the presence of a 24-hour rhythm that retains this average as long as an animal continues to obtain sufficient food. Activity rhythms

TABLE 1. Rhythmicity of individuals in constant darkness, illustrated by the number of hours between highest peaks of activity.

		NUMBER OF DAYS IN DARKNESS																			Average for individuals
	1	2–3	4	5	6	7	8	9	10	11	12	13	14	15	17	28	29	30	34	35	
	Hrs.																				
♀ 1...	–	31	–		19	–	30	–	–	–	–	–	–	–	–	–	–	–	–	–	26.6
♀ 3...	–	24	–		24	21	24	–	–	–	–	–	–	–	–	–	–	–	–	–	23.2
♂ 1...	–	11	–		–		16	–	–		–	–	–	–	–	–	19	26	–	33	23
♂ 9...	–	19	–	–	21	41	18	–	–		25	–	–	–	–	–	–	–	–	–	24.8
♂ 10...	–	17	–	–	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–	–	–
♂ 11...	–	26	26	24	–	–	–	26	–	–	10	–	–	–	–	–	–	–	–	–	22.4
♂ 12...	–	27	–		–		11	39	15	–	–	–	–	–	–	–	–	–	–	–	23
♂ 14...	–	28	–		36	10	29	20	–	–		30	14	33	–	–	–	–	–	–	25
♂ 16...	–	–		33	13	23	26	20	–		27	–		18	–	–	–	–	–	–	22.9
Average for series......		22.9	–	28.5	22.6	23.7	20.6	27.2	20.5	–	20.6	Average for all individuals.............									23.86

are not innate if they break down for animals subjected to illumination and temperature conditions that characterize their period of most intense activity provided such animals continue to obtain normal amounts of nourishment. If fatigue occurs because animals refuse to feed under laboratory conditions, the question of whether an activity rhythm is acquired or inherited would be likely impossible to answer unless nutrition could be administered into the blood stream or perhaps through forced feeding. It is important in investigating this problem for nocturnal animals to have their rhythmic tendencies checked both in continuous darkness and under very weak illumination, but not under brilliant illumination. Rhythms of diurnal animals should be checked by exposing animals continuously to brilliant illumination. Nothing is gained by testing their endogenous rhythmic tendencies in continuous darkness. For tests carried out in darkness, it is also important to know that every measure is taken to create a condition of perfect darkness. It is important to check cabinets and darkrooms for light holes or cracks and this matter should be stated in research papers unless a careful description of dark cabinets is presented. The average photographic darkroom allows "pin-hole light" to enter. Instead of trying to create conditions of perfect darkness which do not occur for most animals, very weak artificial illumination may be reflected continuously from a black surface. Probably the amount of illumination so reflected should be not quite enough to make human vision possible.

Some problems concerning seasonal rhythm:

The question has been raised as to whether considerable periodic inaccuracy in timing of migration is the rule among species of birds that migrate periodically. An affirmative answer has been offered (Phillips 1913). There is some evidence that many species of birds are generally quite accurate in timing their arrival or/and timing their departure at their northern quarters. Also, some birds of tropical Pacific islands are known to restrict their breeding periods to specific times of the year in an environment that scarcely changes at all through the year.

California barn swallows (*Hirundo erythrogaster* Boddaert) that nest at the San Juan Capistrano Mission have been watched by residents of the region for three quarters of a century and have the reputation of ordinarily being accurate in regulation of both time of arrival and time of departure at the Mission (personal communication and *New York Times* index (1930-40). If what is reported is factual, there would be no known explanation for the phenomenon. It is known that some seasonal behavior phenomena have an endogenetic physiological basis. Consider time of shedding of leaves of certain trees transplanted to opposite hemispheres (Stiles 1936) and the timing of hibernation by the beetle, *Cicindela hirticollis* Say (Shelford 1929).

It is unfortunate that taking of written records of the time of arrival and departure of San Juan Capistrano swallows was not undertaken by anyone of scientific reputation many years ago. It is still not clear that carefully written records are being regularly taken through encouragement of any scientific institutions. Other species might be mentioned to illustrate periodic accuracy in timing. The barn swallow is taken for illustration because its reputation for accurate timing has been made by popular observations and writings. It is up to scientists to investigate popular observations and opinions rather than to dismiss them as insignificant before careful investigation is made.

The following problems arise in connection with employment of date as a means to measure timing of activities. Seasonal activities of animals may depend upon: (1) immediate response to environmental changes. Activities in this class may be called *weather controlled* or *climate controlled activities*. For example, some kinds of birds (robins, bluebirds, blackbirds, and meadowlarks) follow the retreat of winter northward. They are "weather migrants" to a certain extent (Peterson 1940) and usually belong to category (3) below. (2) Activities may be directly and immediately dependent upon endogenous influences controlled by other factors than weather. Activities in this class may be called *calendar activities*. Self-controlled physiological timing appears to be illustrated by the beetle, *Cicindela hirticollis* Say. It becomes dormant in August and hibernates all winter. There is no apparent factor in the summer environment to cause this quiescence. Individuals of other associated species do not become quiescent until later (Shelford 1929, p. 154). Most of the more highly migratory birds, especially the tanagers, orioles, the yellow warbler, and other warblers that winter in the tropics, migrate by night and make their passage as if according to a strict schedule on some invisible calendar. They are calendar migrants. Weather does not influence their timing of migration to a great extent. "Adverse conditions might hold them up within narrow limits for several days, perhaps, but on the whole, their punctual arrivals are a never ending source of wonder" (Peterson 1940, p. 526). (3) A complex of endogenous and enviromental influences that are usually quite well synchronized under natural conditions: *composite controlled activities*. This point applies to those birds which regulate their migrations largely through internal (perhaps hormonal) influences and at the same time are influenced by climate at least to the extent that their migratory tendencies are inhibited or eliminated while they are exposed to adverse temperatures that are below certain limits yet sufficiently high to permit locomotion and feeding.

If mean environmental temperatures are important as regulators of timing of migrations, it follows that time of migration correlates with whether seasonal changes occur early or late in the year, and date of the year is an arbitrary consideration irrelevant to this problem. Whether climatic factors are important as regulators in timing migrations must be

known before date of arrival and departure can be considered as a possible basis for judgment of "periodic accuracy" in timing. Date cannot serve as a criterion for judgment of accuracy in timing of activities when climatic factors such as mean temperatures are important as regulators of timing, because different intensities of climatic factors often vary considerably in time of occurrence from year to year. Time may be an arbitrary concept and an artificiality so far as the expression of physicochemical laws is concerned. The changes in external influences to which animals react may appear later in one year than they do in another, and it is the time that such changes occur that usually marks time so far as protoplasm is concerned. These facts invalidate conclusions that weather migrants show periodic inaccuracy in timing migrations (Phillips 1913). This point is worthwhile in connection with applications of Hopkins's law (Hopkins 1918, cf., Shelford 1929, p. 5, 15, Shelford 1930, Lutz 1941, p. 113-114).

To the extent migrations are regulated by independent internal drives, 35.5 days total variation in time of starting or ending a migration amounts to 10 per cent inaccuracy or 90 per cent accuracy for periods of 365 days (the average of intervals that occurs in repetition—not reversal—of migrations in a particular direction). Endogenetic rhythms may be significant even though their peaks vary in time of occurrence by an error of thirty or even more per cent when 100 time units represent the average time space between peaks. Consider the extent that the endogenous nychthemeral locomotor rhythm varies for the crayfish, *Cambarus virilis* (see p. 366 and Table 1). These considerations invalidate conclusions that calendar migrants are not reasonably accurate in timing migrations (Phillips 1913).

Analysis of stomach contents to determine time of feeding.

In order that stomach contents may serve as a criterion for determination of when natural food is eaten, a knowledge of habitat conditions is necessary. Food should not be available as a result of unnatural conditions. Nocturnal beetles have commonly been found in sparrow stomachs. It was at first assumed that sparrows probably secured such nocturnal animals from their natural habitats. It was finally observed that sparrows eat many exhausted or dead animals that fall at the bases of street lights. The fact that artificial light attracts nocturnal beetles explained how it happens that many nocturnal animals are made available to sparrows.

By analyzing stomach contents of wood rats at regular intervals through the day, it was possible to determine the time at which feeding occurred both inside and outside of niches (Spencer 1941). A similar study has been made for hawks and owls (R. Lindeborg 1942, personal communication).

According to Hamilton (1941), experimental methods probably can but rarely if ever reveal what foods mammals normally take from their natural habitats. When it is not possible to employ other methods, the offering to laboratory animals of a great variety of foods taken from their habitats should indicate the probable nature of normal foods. The larvae of the butterfly, *Papilio cresphontes* Cramer do not accept any food plants except those upon which the females of their species are known to deposit eggs (direct observations). This rule does not hold true for *Papilio glaucus* Linn.

PART I. RELATIVE IMPORTANCE OF ENDOGENOUS AND ENVIRONMENTAL INFLUENCES IN GUIDANCE BEHAVIOR

I. Inherited behavior tendency.

II. Inherited tendency modified by acquired features.

III. Completely "acquired" tendency. If determinism is an actuality, then no behavior is completely acquired, and the arrival of inventions is predetermined, perhaps partly as a result of chance but not by "freedom" of thought.

IV. Acquired tendency modified by addition of acquired new features.

Whether environment or heredity are more important in controlling activities is not an important question. It need not be answered, for heredity and environment cannot be separated. All capabilities to carry out acts are inherited. But, not a single ability can function unless offered opportunity by proper environmental conditions. This law applies to activities involved in physiological processes including embryonic development and differentiation as well as to dynamic acts. What activities are carried out by adult organisms and the nature of such activities continues to depend upon both heredity and environment, and to attempt to decide which is more important is like trying to decide whether the motor, or the gasoline and track are more important for the running of a diesel locomotive.

Many activities that are often referred to as acquired are modifications of activities that already exist. Modified tendencies owe part of their characteristics to heredity and part to environmental influences.

Both inherited and acquired tendencies may be modified through (1) learning, (2) changes that accompany aging or development of sexual maturity, (3) imitation of what is seen or learned abstractly, or (4) by way of intelligent or creative activities.

Therefore, behavior does not fall into two natural classes such as inherited behavior and acquired behavior.

The questions of importance are: (1) the extent that environmental stimuli are important in instigation and maintenance of protoplasmic functions, and the extent that endogenous influences function independently of environmental stimulation. (2) The extent that previous experience, learning, and intelligence modify behavior tendencies.

It should be understood that environmental control or environmental guidance does not mean that control in the last analysis is not internal. Control of activities is always fundamentally taken care of

within cytoplasm except when organisms are forced by external means (point 2, p. 371). In some instances, however, activities are at the mercy of environmental stimuli; hence, "environmental control." In other instances, no matter what the environment is like—within normal limits—behavior remains the same; hence, "self-control." In other instances, activities are prompted by internal influences, yet guided by external stimuli, and come under the category of "auto-environmental guidance."

It is convenient to incorporate a consideration of the functions played by cytoplasmic, nervous, and hormonal mechanisms in this classification. When the nervous mechanism is important, the question arises whether consciousness is experienced as activities are carried out. When there is evidence that animals experience consciousness, it is desirable to know whether desire, volition, free will, intelligence and creative thought play a part in controlling their activities.

Typical species behavior (may be modified according to Part J). Atypical behavior is covered by Part K.

I. Environmental regulation (independent of internal drives). Instigation and maintenance of activity are brought about through environmental stimulation. Both instigation and maintenance of activity depend upon stimulation by an environmental influence for the duration of action.

　A. Direct environmental regulation. Direct protoplasmic reaction controls some activities, as when Amoeba reacts to light.

　B. Remote control or indirect environmental regulation.

　　1. Nervous control. Control of activity depends upon nervous activation of effectors. For example, reflexes and deflections. Some chromatophoral activities are regulated through nervous control in turn stimulated by environmental influences. This category pertains to behavior controlled by guiding mechanisms when stimuli lead to predictable responses not dependent upon internal drives. When responses involve internal drives, they belong to the category of auto-environmental guidance.

　　2. Hormonal control. This type of control is not dependent upon transmission of nervous impulses to effectors, although secretions that control activity may be liberated from glands that are activated by nerves. Activities that fall into this class include: growth, some instances of metamorphosis, periodic development of gonads and migrations of some birds when their migratory tendencies are governed by day length; some instances of chromatophoral control.

　　3. Neurohumoral control. This class may be considered a subdivision of point 2 above (Parker 1932, Hanström 1940).

II. Environgenative control. Exogenative control. Externally activated native control. In this class, stimuli that excite initiation of activity originate outside of animals, and the activity is maintained by endogenous tendency. This type of control accounts for breathing in humans in those instances when breathing must be artificially forced at birth.

III. Conditioned control or "endex-environmental control." Endogenous ex-environmental control; that is, endogenetic control dependent upon previous environmental influence. This type of control is characterized by internal influences that depend upon the physiological or psychological state brought about through past environmental influence. Such a state remains for a time after the stimulus responsible for internal change is no longer effective.

　A. Control dependent upon hormonal influences. For example, migratory tendencies that are initiated by changes in day length.

　B. Control dependent directly upon structures altered by modifications during normal growth (see modified growth phenomena).

　C. Control dependent upon nervous conditioning as when behavior is instigated and maintained by memory of objects.

　D. Control dependent upon physiological conditioning. This mechanism accounts for Hopkins's host selection principle when food eaten by larvae consists of plants normally selected by adults.

IV. Self guidance. Self control. Spontaneous behavior.

　A. Native control. Inherited behavior. Virgin behavior independent of environmental stimulation. This category includes behavior controlled by various drives without presence of specific external stimuli while the environment is appropriate for normal activity. For example, activity brought about directly by hunger, and wandering movements adapted to species securement of food or other necessity when no indications of presence of such objects exist. Wandering of newly-hatched wasps leads them to their prey without the wasps having a knowledge of any purpose of their movements and without visual knowledge of what their particular larval host consists. This category includes physiological tendencies to eat, to mate, to secure shelter, and to sleep. Nervous phenomena are usually involved (always involved for many higher animals) if it is assumed that cytoplasm of single-celled animals possesses a nervous property. This category includes those activities that are guided by mental concepts such as thoughts of food, etc., not immediately dependent upon environmental stimulation for their creation or occurrence in mind.

1. Activity dependent upon hormone.
   a. Through direct nervous control; for example, singing in canaries (Shoemaker 1939).
   b. Independent of direct nervous control; for example, some aspects of metamorphosis (Hanström 1940).
2. Activity independent of hormones; for example, securement of shelter through secretory activity or by secretion and passive selection, locomotor movements of plankton organisms, some examples of nomadism, spontaneous locomotion of Amoeba.

B. Acquired behavior. Behavior in this category is entirely new for individuals. Acts may be acquired in at least three ways.
   1. Acquirement through learning (memory).
      a. Acquirement by imitation; for instance, smoking.
         (1) Imitation of that which is directly observed.
         (2) Imitation of that which is learned through abstraction, as by way of communication.
      b. Acquirement by accidental experience, as when trial-and-error actions that are successful are repeated.
   2. Acquirement by invention. Smoking originated as an invented act.

V. Auto-environmental guidance. Behavior tendency may be inherited or acquired. Environmental stimulation is important, but activity is not always an immediate result of environmental stimulation for any particular stimulus. Self-guidance and environmental influence and usually nervous phenomena are involved. Nervous phenomena may be said to be always involved when it is presumed that cytoplasm possesses a nervous property. Nerves of animals have developed through the improvement of a nervous property already characterized by cytoplasm.

A. Activity independent of hormonal control. This class includes homing of limpets, many trial-and-error actions, and activities guided by such complexes as hunger plus observance of food. See learning, p. 27 and modified behavior, Part J.

B. Activity under humoral control or regulation. The extent that an animal tends to dominate others before opportunity occurs for the nature of other individuals of a group to be learned illustrates an instance of guidance partly by the appearance of objects in the environment and in part by an endogenous tendency controlled by a physiological mechanism. [Another factor—modification of behavior through learning—occurs when an animal's attempts to dominate other individuals are unsuccessful and when it is domineered by other individuals. See references on social

hierarchy including "peck order" (Allee 1931)].

PART J.   MODIFIED BEHAVIOR

For clarification of abnormal behavior, see Part K. References: physiology and psychology texts.

This category differs from acquired tendency and acquired action. Acquired tendencies and actions are entirely new to individuals. They are—in a sense—modifications in native behavior but are not modifications of specific tendencies or acts already existent. Modifications in native behavior that are completely new belong to the category of *Innovation* (Part B, Div. 2, V). "Modifications" in this outline apply especially to particular tendencies and actions that already exist.

Many modifications occur for behavior tendencies that are inherited. Other modifications occur for actions that are previously acquired or inherited and already modified to some extent.

Not all modifications are "acquired" in the usual sense as through imitation or learning. Modifications in behavior may occur as a result of changes that accompany aging and senescence, development of sexual maturity, injury, metamorphosis, or in accordance with what opportunity offers to behavior expression. Modification in some behavior traits occurs through other types of experience than behavior experience, as illustrated by certain influences of physiological or growth experience. Modifications of behavior for some animals may be acquired by way of physiological or/and psychological adjustment and may depend upon invention of new features of action.

Modifications listed below may apply to any of the categories of behavior listed elsewhere in this outline. There are no behavior traits which are immune to modification influences.

Endogenous changes are often but not always brought about by environmental forces or changes. Some endogenous modifications occur as a result of internal changes that are independent of environmental changes so long as environmental conditions remain normal.

All individual behavior is typical for individuals since the behavior of individuals follows laws that depend upon (1) inheritance, (2) the nature of opportunity that is available for expression of inherited tendency, and (3) change of initial inherited tendency by direct or past environmental influence. The end results would probably always be predictable for normal individuals, and therefore be typical for species if all facts could be known concerning the heredity, past experience and its modification of behavior tendencies, and nature of all environmental opportunities that are available to individuals previous to the point of behavior analysis.

I. Environmental regulation of modification.

A. Modification by absence or rarity of objects normally used. When environmental objects are lacking that are normally used, normal behavior is modified. Environmental influ-

ence may in this manner cause modification in behavior concerned with construction of shelters when exogenetic materials are employed. The same rule applies to substitution of foods.

   1. Modification by substitution of different objects. Some carnivores will eat vegetation rather than starve.

   2. Modification by substitution of a new act; for example, migration from areas in which food is scarce or absent.

   3. Modification by inhibition. Animals do not eat when no food is available.

B. Modification by extent of availability or intensity of influences.

   1. Free modification. The behavior of animals after they are washed into caves is not normal in some respects. It is modified in part by the alteration of environmental conditions. To be treated comprehensively, this subject would need to cover the influence that all environmental factors can bring about in behavior, depending upon an animal's contact with light, water, food, enemies, drugs, pressures, etc.

   2. Forced modification. Behavior forced by environmental mechanisms. An animal's behavior can be modified by trap mechanisms or other environmental forces to the extent of inhibition of all activities (death). Modification of behavior by mere exposure to predators is not in itself forced by external means. Animals may be carried by winds, hurricanes, and currents, etc.

     a. Forced activation; for example, seed filaments of Stipa are forced to curl as a result of desiccation so that the seeds are pushed into soil (Coulter et al. 1931, p. 445).

     b. Forced inhibition of movement; occurs when animals are frozen in ice.

C. Modification according to number of influences that are effective simultaneously. See modifications by supplementation, antagonism, and conversion. Confusion is one type of modification that occurs when a number of stimuli are present at once.

II. Change in behavior through direct environmental modification of physiological phenomena (includes modification of vitality and growth phenomena, Part G). In this category modification occurs as a result of internal changes that are in some way closely dependent upon influences that come from the environment.

A. Direct environmental modification of vital physiological processes.

   1. Modification by alteration in availability of oxygen to respiratory (including circulatory) systems.

   2. Modification by alteration of availability of water to surfaces of animals (when direct contact with water is normally required for locomotion or osmotic processes, etc.).

   3. Modification by injury or obliteration of mechanisms, as when organs are amputated (belongs in Part K).

   4. Modification by temperature. Temperature modifies viscosity of protoplasm and circulation fluids, surface tension, osmotic mechanisms, etc. Modification of such processes changes behavior—especially in regard to rate of processes. Extreme consequences are injury, inhibition of action, death.

   5. Modification by pressure. External osmotic concentrations influence osmotic processes (Krogh 1939, 1941).

   6. Modification by circulatory disturbances, as when viper venom enters the blood stream of mammals (Harris 1938).

   7. Modification by digestive disturbance, as when poisons are eaten that cause indigestion, regurgitation, etc.

B. Direct modification of nervous phenomena.

   1. Through modification of receptors. Overstimulation may be injurious and may cause increase or decrease in sensitivity of receptors. Consider the influence of overstimulation of the eyes of man by bright light. Understimulation can cause degeneration of sense organs, and stimulation may be required for maintenance of receptors (Noble 1931, cf., Hesse 1937, p. 533). Extent of sensitivity also depends upon the extent that receptors have been conditioned to stimuli of normal intensity.

   2. Through modification of the principal nervous center.

     a. Modification by chemical influence.

       (1) Modification by invigoration of particular mental functions, as by intoxication.

       (2) Modification by inhibition of special or all mental functions by narcotics or other specific chemicals.

       (3) Modification of sensitization, as by alcohol.

     b. Modification by pressure, as received by blows or skull fractures, as when followed by coma or insanity.

     c. Modification by temperature, as delirium that accompanies high fevers.

     d. Modification dependent upon direct nervous stimulation received through sympathetic or other nerves.

       (1) Modification dependent upon extent of present stimulation.

         (a) Overstimulation (either in intensity or duration of stimuli); for example, temporary insanity due to excessive pain.

       (b) Understimulation either in intensity or duration of stimuli. Some instances of stupor, hypnosis, and sleep.

     (2) Modification dependent upon previous experience.

       (a) Overstimulation (either in intensity or duration of stimuli). For instance, some types of insanity, shell shock, knock-outs by way of the solar plexus.

       (b) Understimulation (either in intensity or duration of stimuli). Some instances of stupidity and mental degeneration.

   c. Modification dependent upon thought obsessions, fears, and disappointments caused by overstrengthening of thought associations.

     (1) Modification dependent upon present overstimulation; for example, some instances of temporary and curable insanity.

     (2) Modification dependent upon previous overstimulation; for instance, some forms of insanity.

3. Through modification of nerve paths that extend between nervous centers and receptors or effectors.

   a. Modification by chemical influence.

     (1) Modification by invigoration as by stimulants.

     (2) Modification by inhibition or obliteration; for example, as by the influence of curare upon synapses.

     (3) Modification by alteration in extent of sensitization.

     (4) Modification by chemical antagonism or counteraction.

     (5) Modification as a result of activity of nerves. Modifications may occur for points (3) and (4) as a result of nervous activity. Fatigue and strengthening effects of nervous or neurohumoral action belong to "endogenous regulation of behavior" modification noted below, yet are often dependent upon environmental influence as mentioned above under "environmental regulation of modification."

       (a) Overactivity may lead to delayed action or inhibition.

       (b) Underactivity may lead to degeneration of nerve paths and incapacitation to perform acts that depend upon the nerves.

   b. Modification by pressure. For example, nervous impulses can be initiated by pressure exerted upon nerves as may occur when vertebrae are dislocated.

   c. Modification by obliteration, as when limbs are amputated or when nerves are severed (Part K).

4. Through change in the complexity of nervous impulses received by a principal adjustor.

   a. Modification by supplementary influences. One type of stimulus may support another type of influence [see guiding mechanisms (Part D) in regard to physiological-mental mechanisms and compound mental mechanisms].

   b. Modification by antagonistic influence. One type of mechanism may dominate another when two or more act simultaneously. This phenomenon may cause apparent reversal of an action (see factors that may cause variations in research results).

   c. Modification by conversion influence. A particular kind of stimulus may bring about a change in the original nature of a response even to the extent of reversal (see point 2, p. 398). It is usually difficult to distinguish between antagonistic and conversion influences unless special experiments are conducted to answer the problem. It is also sometimes difficult or impossible to know whether or not reversal of an action tendency such as change from a positive response to a negative response is due to previous conditioning (Welsh 1930).

5. Through modification of effectors (illustrated by modification of muscles).

   a. Modification according to extent of use.

     (1) Overuse may lead to high development or injury.

     (2) Normal use leads to normal development.

     (3) Underuse leads to weakness.

     (4) Lack of use may cause atrophy.

   b. Modification according to extent of strain. (Subdivisions follow those of a.)

   c. Modification according to chemical influences as when poisons enter the body.

   d. Miscellaneous. Modification by injury or obliteration (Part K).

III. Endogenous regulation of behavior modification. Endogenous modification of behavior may or may not be dependent upon environmental changes.

A. Modification that accompanies life history processes; or, the result of time on the expression of heredity.

1. Modification that accompanies metamorphosis, growth, and differentiation.

2. Modification that accompanies aging and senescence.

3. Modification that accompanies reaching of sexual maturity.

B. Modification as a direct consequence of action or stimulation. The modification is dependent upon chemical or physico-chemical changes. This type of modification may form nervous associations but is not the process of carrying out actions.

1. Fatigue effect. The maximum extent of influence is inhibition.

2. Exhaustion effect. Substances from which energy is obtained, or oxygen supply, or secretions that are products of cellular activity may become exhausted. The maximum extent of influence is inhibition or death.

3. Shock effect; that is, nervous shock. Shell shock serves as an example.

4. Strengthening effect. Nervous paths, muscles, and mental mechanisms are strengthened through use. Strengthening effects may be the result of the influence of stimulation upon growth phenomena, or may be due to release of stimulating or invigorating chemicals by cells, or may be due to reduction of resistance forces by stimulation factors. This type of phenomenon is illustrated by the formation of all types of nervous associations including thought associations. Nervous associations may be classified as follows:

a. Basic nervous association. Abstractions are not involved.
  (1) Internal association: muscular memory (Pieron 1913, cf., Pearse 1939).
  (2) Environmental-internal association: as the nervous association that permits homing of limpets (cf., Holmes 1911).

b. Semi-abstract association or physiological-abstract association. An association is formed between an abstraction (such as images of food) and an activity (such as secretion by salivary glands or a tendency to locomote towards images of food). This phenomenon illustrates the formation of associations upon which deflected actions ("conditioned reflexes") depend.

c. Semi-abstract substitution association or physiological-abstract duplication association. If a bell is rung when a dog sees food, the sound of the bell forms a nervous association between the sight of food and the ring of the bell. The visual image symbol of food is duplicated by a sound symbol. This is another type of deflected action ("conditioned reflex") mechanism. In semi-abstract duplication associations, one symbol duplicates another through a nervous association and a physiological process is prompted by a stimulus associated with the substituted symbol.

d. Abstract associations are purely mental associations such as thought associations; thoughts may be immediately dependent upon stimuli for their formation. In the sense used here, mental images created through optical stimuli are among the types of thoughts that are possible.

C. Modification through physiological and/or psychological conditioning. Many important activities that are modified in this class belong to endex-environmental control. It is sometimes impossible to determine whether psychological phenomena are involved in conditioning of animals to stimuli. Even when modification is undoubtedly psychological, it is not always clear whether modification is by way of subconscious learning or through consciousness. It is therefore safer and not incorrect to include psychological processes within the scope of physiology since mental processes have a physico-chemical basis. If a phenomenon is known to be mental, it is more specific to refer to it as a mental phenomenon.

1. Conditioning through past physiological experience other than nervous experience.
  a. Modification in selective tendency.
    (1) Partial modification. In some instances native behavior tendency is only partly dominated by modified physiological state. For instance, most lepidoptera behave in accordance with Hopkins's host selection principle but to a limited extent (Imms 1940, p. 286).
    (2) Complete modification. Host selection for some insects is controlled through what organisms feed upon during their larval stage. This phenomenon is unlike a "conditioned response" because radical changes occur in sense receptors and other organs (Imms 1940, p. 286, 318). It is suggested that this phenomenon is made possible by sensitization of the antennal chemoreceptors and that such sensitization is controlled by the presence of specific chemicals obtained during the larval stage. The problem is being attacked by interchanging antennal chambers of pupae formed from larvae conditioned to different kinds of plants (unpublished research). Modification in selective tendency occurs only when larvae feed upon new kinds of plants not normally fed upon.
  b. Modification in timing action. Modification of action by influence of past physiological experience upon the rate at which energies are built up and released.

The fundamental forces of nature are not rhythmic although they may be cyclic. Fundamental natural forces are constant at any definite complex of conditions. It is probable that all inanimate rhythms and all biotic spontaneous rhythms depend upon two influences for their periodicity: (1) fairly constant and gradual increase in an energy that acts towards a direction of escape, and (2) resistance to this energy that is overcome when energy reaches a point above a certain threshold. The resistances tend to be constant. These mechanical functions explain why water drips rhythmically from a faucet when the rate of flow is properly regulated. The energies behind the water (water pressure and gravity) are constant. The resistances are cohesion and surface tension forces. When pull of weight increases to points that outweigh cohesion and surface tension forces, release occurs and the phenomenon repeats itself. The same explanations hold for spontaneous biological rhythms. When resistance is never complete and when some release of energy tends to be perpetual, rhythms may not at first appear to be a result of these functions. Consider the formation of waves and tides. Rhythms such as cellular motion are results of spontaneous impulses plus activation. Each wave begins spontaneously and it is only this spontaneous aspect that follows the laws mentioned. An example of modified timing is offered by composite rhythms (Part H). Periodic activity of whole animals must depend upon cells in which energies increase. Cell membranes probably offer the necessary resistance for the production of rhythmic influences. The following types of activity rhythms are theoretically possible: (1) periodic activation of protoplasm that tends to be immobile, (2) periodic inhibition of protoplasm that tends to be perpetually mobile, (3) (1) plus (2).

2. Conditioning through previous nervous experience.
   a. Modification by increase in efficiency.
      (1) By way of elimination of random movements.
      (2) By way of increase in rate of action.
      (3) Miscellaneous modifications.
   b. Modification by compensation as, for example, asymmetrical compensation. When a functional mechanism is partly injured or partly obliterated on one side of the body as by blocking out of a receptor, an asymmetrical compensation adjustment may take place so that the end result that would originally have been accomplished is still achieved. When one ductless gland of a pair such as an adrenal is injured, the other gland may compensate for it. This instinctive phenomenon occurs when robber-flies react to light after one eye is blackened (Loeb 1918).

   c. Modification by substitution following partial or complete obliteration of a mechanism due to injury (Kühl 1932). This type of modification occurs when a new mechanism is relied upon that is normally superfluous or undeveloped. This phenomenon occurs for some guidance mechanisms. Blind persons may rely upon touch for guidance. Some blind persons subconsciously learn the vibration production audio-reaction complex mechanism.

   d. Modification by availability of product of action or basic stimulus essential for the excitation of complex instinct. The point at which a complex instinct begins often depends upon what link of action is stimulated. Hens and rough-winged swallows construct their own shelters if none are available but usually accept shelters that already exist when they are constructed in accordance with the nature demanded by the species.

   e. Modification by previous personal or environmentally constructed experience of the principal nervous center. That is, through learning accomplished by principal nervous centers. This phenomenon is important in guidance of selectivity.

      (1) Through construction of perceptions guided by external influence, as modification by automatic imitation of mental experience created by perceptions of environmental phenomena. Some birds modify their songs according to the sounds they hear.

      (2) Modification by thought associations or formation of symbols.

         (a) Formed by personal experience. Acts tend to be repeated when accidental actions or acts "tried" are successful or when they produce mental symbols that represent satisfaction. Keas continued to eat fat after trying it (Borradaile 1923, p. 308). Chicks peck at all objects and in this way finally learn to distinguish food from other objects (Loeser 1940). Peck order tendencies are modified in accordance with what is learned of the extent of aggressiveness of other individuals.

(b) Formed by what is implied by the actions of others. Learning by imitation.

(c) Formed through construction of ideas received by way of communication.

1) When mental association between act and result is understood. Active acceptance of advice.

2) When mental association between an action and its result is lacking; for example, mental association of punishment or rewards in relation to acts serve as substituted symbols.

f. Modification by invention of new features. For example, the use of forks, chopsticks, etc., was an innovated modification of a native act for the persons who invented their use. To put things in the mouth is instinctive. The use of forks is usually learned by way of points 2, e, (2), (b) and (c) covered immediately above.

g. Transfer of training.

PART K. "ABNORMAL BEHAVIOR"

Abnormal behavior probably does not exist in many of those instances ordinarily considered as abnormal. Behavior that is not typical of most individuals of a definite age and sex is often the result of unusual experience. In such instances, it is the experience and not the product of experience which is unnatural. A portion of the men who become insane—including those who attempt suicide—as a result of war experiences or similar trying experiences are normal persons, and their consequent atypical behavior should be regarded as a normal product of certain specific types of experience. Atypical behavior that comes about due to weakness in mental adjustment following the usual disappointments, nervous shocks, and fears likely to be confronted by a majority of persons falls under the category of abnormal behavior. The point is that many actions cannot be classified as abnormal or normal, because so much depends upon past experience (News Week 1936, Dorsey 1925, Garrett 1930, Devine 1933, Hart 1934, Davis 1937, Valentine 1938, Cole 1939, Doreus & Shaffer 1939, Brown & Menninger 1940, Lawson 1940). "Abnormal" behavior is due to structural defects of the brain (mind) or to defects of other parts of an organism. These defects may be caused by mutations, by hereditary flaws in genes or by injuries such as those brought about by pathological conditions; or they may be the result of abnormal environments during or following embryonic development (Barker & Sprunt 1925, Amer. Med. Assoc. 1935, Sturtevant & Beadle 1939, Yapp 1939). Some atypical features of behavior are listed under Modification of Behavior (Part J).

PART L. PHYSIOLOGICAL FUNCTIONS OF AGGREGATIONS (ALLEE 1931)

[2] ADJUSTMENT IN BEHAVIOR AND PSYCHOLOGICAL STATE

See [1], Part G.

[3] MODIFICATION OF BEHAVIOR

See [1], Parts F., J.

[4] TIMING OF ACTIVITIES

Nocturnal, crepuscular, diurnal, and auroral activities have been discussed (Crawford 1931, Thompson 1931, 1932, Elton 1935, Carpenter 1935, Park 1939). Some animals are believed to be strictly crepuscular; for example, certain tropical owl butterflies (Hammerton 1930). Their locomotor activity is rhythmic, yet neither definitely nocturnal or diurnal. It occurs under a complex of environmental conditions intermediate between extremes of day and night. It is not scientific to consider intermediate conditions within one complex of extreme conditions any more than to regard them as belonging within the opposite extreme. Probably, crepuscular activity is to be conceived as a separate category for some animals. Dawn may prove to be a distinct time for activity for some species. Certain activities of some organisms probably consist of two peaks and two rest periods for each twenty-four hours. This tends to hold true for the locomotor and feeding activities of some species of Caprimulgidae (Eaton 1910, 1914) and Caligo owl butterflies (W. J. Gerhard 1942, personal communication).

A conception of locality communities being somewhat divided into time associations (time "communities" of Elton) has been presented (Elton 1935, Park 1935).

Seasonal faunas have been outlined according to abundance of active species: prevernal, vernal, aestival, serotinal, hiemal, and perennial animals or societies (Shelford 1937, Shackleford 1929, Clements & Shelford 1939). The same adjectives may be applied to activities as they occur in or are restricted to various seasons.

Recognition has also been given to animals that are temporarily active in a community while passing through it: "permeants" (Clements & Shelford 1939).

[5] PLACE RELATIONSHIPS

Div. 1. Activities characterized by type of environment.

Activities vary according to the types of environments in which they occur; that is, according to the features of environment to which activities must be adapted and adjusted.

Amphibians divide their time between aquatic and terrestrial activities each class of which is open to further subclassification. Some kinds of animals such as many species of the butterfly Argynnis (Holland 1931) divide their activities between forest and grassland. Other combinations of activities

that occur for various animals are forest-tundra, grassland-desert, aerial-terrestrial, aerial-aquatic, terrestrial-aquatic-aerial as for some diving birds, terranean-arboreal, terranean-subterranean, terranean-subterranean-arboreal activities. Refer to classifications of habitats according to their biotic and physical peculiarities (Shelford 1937, Pearse 1939, p. 223-229, Clements & Shelford 1939).

   I. Aerial activities.
  II. Aquatic activities.
 III. Terrestrial activities.
    A. Supra-terranean activities.
      1. Arboreal activities.
      2. Shrub or herbal activities.
    B. Terranean activities.
    C. Subterranean activities.

    A. Tundra activities.
    B. Desert activities.
    C. Grassland activities.
    D. Forest activities.
      1. In deciduous forest.
      2. In coniferous forest.
      3. In broad-leaved sclerophyll forest.

      1. In temperate forest.
      2. In tropical forest.

    A. Arctic-Alpine zonal activities.
    B. Hudsonian zonal activities, etc.

Div. 2. Movement of organisms (Fig. 9).
Movement of organisms in their environment concerns means of species dispersal and changes of immediate environmental spatial relations.

   I. Convection. Passive conveyance.
    A. Entrapment of energy. Current trapping.
      1. Entrapment of wind.
        a. Passive entrapment. Aerial conveyance; occurs for parachute seeds and winged seeds.
        b. Active entrapment.
          (1) Wind riding ("parachuting"); occurs for spiders that spin "wings" (Kinsey 1938).
          (2) Soaring; occurs for certain birds. Orientation in soaring is accomplished through employment of special gliding mechanisms (B, 2). Continuous activity of organisms carried is involved.
      2. Entrapment of water currents.
        a. Flotation.
          (1) Passive securement of buoyancy; for example, Pectinatella and cocoanuts.
          (2) Active securement of buoyancy; for example, some mollusks.
        b. Locomotion; as for plankton organisms that locomote. Organisms that locomote sufficiently rapidly to prevent water currents from controlling their movements cannot be properly classified as plankton. Cladocera and Copepods are nekton when

they occur in ponds that cover but a few feet of territory.
      3. Attachment to organisms or within organisms.
        a. Passive attachment; occurs for Pectinatella, hooked and spiny seeds of many plants, eggs of parasites.
        b. Active attachment; occurs for ticks, leeches, Remora, hookworms, cercaria.
    B. Conveyance by gliding on ambient medium. Conveyance and guidance depend fundamentally upon employment—usually active employment—of gliding mechanisms. This point overlaps with entrapment of energy (A) and II.
      1. Passive gliding; occurs for a tropical spider (Lull 1929).
      2. Active gliding; occurs for a species of tree frog, snake, lizard, several rodents, "flying" lemur (Lull 1929, Hammerton 1930).
  II. Active conveyance. Locomotion. Manner of locomotion depends upon what medium of propulsive force is exerted and upon what method or methods are employed to expend energy.
    A. Propulsive force acts against water medium.
      1. Swimming. Diving denotes locomotion carried out under water by organisms that live mostly on water or out of water. Propulsive force is exerted in water more than on water.
        a. Appendicular propulsion.
          (1) Organic propulsion: as occurs for the Gyrinidae, fishes, penguins, water ouzel, etc.
          (2) Organellular propulsion.
            (a) Pulling; demonstrated by the use of flagellae by Mastigophora.
            (b) Pushing; demonstrated by the infusoria.
            (c) Pulling and pushing; illustrated by some colonial flagellates.
        b. Propulsion by squirting. Propulsive force is exerted through employment of the bellows principle; for example, occurs for squids and dragon-fly nymphs.
        c. Undulatory propulsion.
          (1) Cellular undulation.
          (2) Body undulation.
            (a) Axial winding; occurs for eels, sea snakes, and some worms.
            (b) Lateral-winding; occurs for Chironomid larvae.
        d. Secretory propulsion; occurs for gregarines.
      2. Walking or running. Propulsive force is exerted on the surface of water; occurs for Gerridae and basalisk lizards.
    B. Propulsive force exerted against solid medium.
      1. Propulsion exerted by pushing ambient medium. Excavation. Fossorial locomotion; occurs for moles and mole crickets. Locomotion fits point 2 when animals move

through pathways independently of the pull exerted by burrowing activities.

2. Propulsive force is exerted upon solid or semisolid surfaces such as surface tension films.

  a. Protoplasmic flow: Amoeboid movement. Pseudopodial phenomena may be involved such as alternation of gel and sol. Rolling occurs for some amoebae.

  b. Appendicular propulsion: force exerted directly by appendages.

    (1) Organic propulsion. Locomotion is accomplished by organs.

      (a) Walking. Running, if rate is above normal. Locomotion depends upon (1) leg movements, (2) spine movements, (3) employment of pulling-tubes (pulling-tube locomotion); occurs for echinoderms.

      (b) Springing (jumping or leaping). Locomotion may be accomplished by means of legs or abdominal springs; as occurs for kangaroos and collembola.

    (2) Tissue appendicular propulsion; occurs for Planaria.

    (3) Organellular propulsion. Ciliary propulsion occurs for Trichodina.

  c. Measure-shoving, shoving, or measuring; that is, geometrid locomotion; occurs for Hydra and many caterpillars. Termed looping when movements are sufficiently exaggerated in extent to form body loops.

  d. Somersaulting; occurs for Hydra.

  e. Undulation. "Gliding."

    (1) Tissue undulation; occurs for snails and large polyps.

    (2) Body undulation.

      (a) Axial winding; demonstrated by worms and snakes.

      (b) Side winding; occurs for the sidewinder snake.

  f. Peristalsis: illustrated by locomotion of some flagellates and Planaria.

  g. Swinging and release of anchorage. Propulsive force for locomotion is obtained from kinetic physical energy obtained through the influence of gravity upon bodies permitted to fall. This type of locomotion occurs for gibbons.

  h. Complex locomotor mechanisms that often function simultaneously or in rapid alternation.

    (1) Organellular plus peristaltic propulpulsion (Planaria).

    (2) Shoving plus appendicular propulsion (Hydra, some caterpillars).

    (3) Undulatory plus appendicular propulsion (some salamanders).

C. Flight. Propulsive force is exerted upon air. Gliding or parachuting are believed to precede flight in its stages of evolution. Probably flight may be either preceded or followed by soaring ability.

Aerial locomotion has developed in animals of the following groups: spiders, insects, fishes, frogs, snakes, lizards, birds, bats, rodents, Dermaptera, etc. (Lull 1929, Hesse 1937). Flight has evolved in the following categories: insects, extinct reptiles, fish, birds, bats. Jumping and swinging and "wind riding" of some animals approaches aerial locomotion; for instance, Collembola, gibbons, and spiders (Lull 1929).

D. Complex locomotion. Propulsive forces may be exerted against more than one type of medium at the same time. The Sargassum fish, water ouzel, and octopus can half walk and half swim at the same time.

E. Compound locomotor mechanisms that may occur alternately.

  1. Swimming and walking; for example, polar bears.

  2. Swimming and flight; for example, flying fishes.

  3. Walking and flight; for example, passerine birds.

  4. Walking, swimming, and flight; for example, ducks.

III. Compound passive and active conveyances involved simultaneously. Many plankton organisms depend upon locomotion and upon water currents for their distribution.

IV. Combination of passive and active means of conveyances. Birds that fly and soar alternate active and passive methods of conveyance. To the extent that soaring is oriented and maintained by gliding, it is—in itself—an activity. Soaring in itself—when not modified by gliding—permits conveyance by air currents. Conveyance by unmodified soaring is carried out passively. The entrapment of air is carried out through active employment of wings in soaring and gliding of many birds and insects.

Migration

Migration is a special aspect of locomotion. Migration depends upon locomotor mechanisms and amounts to (1) movement from one type of environment to the same kind of environment in those instances in which crossing or penetration of a different type of habitat is involved, (2) may amount to movement from one kind of habitat to a different type, or (3) may be nomadic locomotion (Webster) in those instances in which movement is not practically continuous. Migrations may be classified according to the factors that assist organisms in orientation ([1], Part C, D, and E). They may also be classified according to the environmental and endogenous influences that are responsible for instigation and main-

tenance of migratory movements (Part H, seasonal rhythms).

  I. Horizontal migration (Wetmore 1926, Williams 1930, Heape 1931, Lincoln 1938, Allen 1939, Pearse 1939, Hitchcock 1940, Griffin 1940, Mayer 1940, cf., Peterson 1940, 1941, Warden et al. 1940, Powers 1941).

  II. Vertical migration. Vertical migration is known to occur at periodic intervals for many organisms including copepods and other plankton organisms (Loeb 1893, Jennings 1906, Franz 1911, Schallek 1942), rotifers (Jennings 1900, cf., Shelford 1937), certain spiders (Sanders & Shelford 1922, cf., Carpenter 1928), pentatomid, Menecles (Park & Strohecker 1935), and the milliped, *Spirobolus marginatus*. Horizontal migrations bring about a modification in the biotic composition of communities, and vertical migrations change the biotic constituency of stratal socies. Such changes tend to modify food relations among organisms.

Div. 3. Procurement of shelter.

There are at least six aspects of activity concerned with securement of shelter: (a) securement of general habitat, (b) whether securement is a passive result, or the result of activity of the animal receiving the benefit of cover, (c) whether securement is directly or indirectly obtained, (e) what drive (or function) is responsible for activity involved in securing shelter, (e) what environmental influences are involved in guiding an animal to a suitable environment and to objects suitable for use in construction of shelter; this point is covered by classification number [1]D, (f) whether the building of shelter involves the use of materials and if so, whether body-derived materials or extraneous materials or both are involved. Points a and e are best treated in separate classifications, subdivisions of which may depend upon remaining standpoints (b, c, d, f). Points b, c, and f fit satisfactorily into a single classification. The classifications follow according to the various standpoints mentioned.

Section 1. Procurement of habitat (based on a).
I. Passive procurement.
  A. "Accidental" procurement, that is, accidental conveyance.
    1. Through physical factor such as wind.
    2. Through biotic factor. Parasites gain entrance to hosts by being eaten from the inanimate environment.
  B. Placement.
    1. By individuals of a species as through oviposition.
    2. By individuals of another species adapted for transporting a rider to a new host, as for insect transmission by way of biting, or, by hosts egesting a rider into the outer environment.
  C. Indirect procurement; occurs for parasites that change hosts through primary hosts feeding upon secondary hosts.

  D. Growth and physiological adaptation, for example, development of hydrostatic organs by certain pelagic hydroids, barnacles, and such mollusks as *Ianthina fragilis* (Borradaile 1923).

II. Active securement; that is, through locomotion, etc.

Section 2. Procurement of shelter for self or/and possessions (based on b, c, f). Nests and other shelters constructed by organisms are records of behavior (Peckham 1898, 1905, Hartman 1905, 1913, Fabre 1918, etc., Borradaile 1923, Ealand 1926, Jones 1927, 1929, Hammerton 1930, Mills 1932, Schmidt 1934, Needham 1935, Kinsey 1936, Emerson & Fish 1937, Emerson 1938, Cory 1940, Felt 1940, and texts on anthropology and human geography). Pellets are a record of behavior also and usually indicate an animal's presence within habitats of reasonable dimensions (Taylor 1930b, cf., Clements & Shelford 1939).

I. Passive procurement.
  A. Without involvement of physiological activity on part of the animal receiving benefit of shelter.
    1. Through placement. Animals may be placed in relation to niches, or shelters may be built around individuals, or both activities may occur. Both biotic and physical securement may be subdivided according to whether selection of habitat by parent or host is specific or non-specific.
    a. Biotic procurement. Biotic environment serves as shelter.
      (1) Direct procurement. Direct securement is obtained for the young of the bitterling, parasites and commensals when reproduced within a host, eggs and newly hatched larvae of plant-boring insects, certain amphibia, for example, the Surinam toad, and obstetric toad, young in brood pouches of marsupials or the sea horse or Daphnia, etc., eggs or immature covered through "incubation," or through being covered by many individuals as occurs for the immature of Eciton.
      (2) Indirect procurement through evolutionary involvement of other species among community members as occurs for parasites that change hosts when one of their hosts is eaten.
    b. Physical procurement. Physical environment serves as shelter.
      (1) Direct procurement. Securement may be only species dependent as for robins, or may be community dependent as for cowbirds.
        (a) Placement of individuals in a niche as when eggs are laid in a concealed place.

    (b) Formation of shelter around individuals; for example, skate egg cases. This is accomplished by passive physiological activity or by dynamic behavior, or by passive activity followed by dynamic action, for example, as occurs in the formation of egg cases and egg-baskets of spiders. Criteria (a) and (b) are also appropriate under biotic securement 1, a, (1).

    (2) Accidental procurement as by precipitation. For example, some of the eggs of cod fish reach secluded places following their release.

  2. Evolvement of adaptations to habitats in which predators are helpless.

    a. Remaining in dark habitats, e.g., cave and deep sea animals.

    b. Remaining in habitats devoid of predators, e.g., parasites of dominant carnivores, organisms of hot springs.

B. Through involvement of physiological activity, that is, secretory activity.

  1. Direct securement as occurs for Coleps, ostracods, pupa cases, oysters, and snails. Both epiphragms and shells of snails are results of this type of securement.

  2. Indirect securement as occurs for gall-insect larvae.

II. Physiological activity in collaboration with passive or automatic selection of environmental material (locomotion not necessarily involved). This type of shelter securement occurs for Difflugia, Floscularia (Melicerta), and might take place for Cistenides.

III. Active securement.

A. Through submersion as occurs for tapirs (related to points E and F).

B. Through attachment to organisms prepared to attack aggressors, as occurs for Remora and Melia, the "polyp crab." See anchorage mechanisms.

C. Through creation of dark habitat. Creation of turbidity as accomplished by crayfish.

D. Through finding and fitting into niches (modification of environment is not involved).

  1. Physical selection.

    a. Independent of biotic construction as occurs for black bears.

    b. Dependent upon biotic construction as occurs for hermit crabs.

  2. Biotic selection. For instance, chicks go under a hen for shelter.

E. Through construction (on part of the individual receiving benefit for itself or possessions). Active modification of environment is involved as well as complex behavior of the individuals that obtain shelter either for self

or "possessions" or for both self and possessions.

  1. Excavation or burrowing (materials not used for construction).

    a. In biotic habitats. This category includes tunnelling, dissolution, and digestion (a coaction). This type of shelter securement occurs for Sacculina.

    b. In physical habitats. This category includes fossorial behavior, carving (a reaction). This type of behavior occurs for kangaroo rats.

    c. In physico-biotic habitats. This category may involve carving or dissolution, etc. This type of behavior occurs for oyster sponges and woodpeckers (as when food channels or food storage cavities are made). This category of behavior is illustrated whenever cavities penetrate both secreted shelters and living tissue.

  2. Construction through use of materials. Each of the following classes may be subdivided according to whether: (1) ground, (2) cliffs, or (3) various types of objects [(a) living or (b) inanimate] serve to support shelters. Intergradation exists from points a through c.

    a. Through use of indigenous material as occurs for orb weavers and octopuses. So far as the shelter function is concerned, some spider webs are equivalent to the ink screens of octopuses.

    b. Through use of indigenous material and exogenetic material.

      (1) Use of endogenous material most important. Some caterpillars illustrate this point by the manner in which they construct nests and cocoons.

      (2) Use of endogenetic and exogenetic materials about equally important as holds true for caddis-fly larvae, labyrinth fishes, and sticklebacks.

      (3) Use of exogenetic material or materials most important. For example, many birds.

    c. Through use of exogenetic material only. Humans illustrate this type of shelter securement in the construction of various types of shelters. The same type of behavior occurs for alligators as they construct nests for their eggs.

  3. Excavation and construction with materials in combination. The construction of nests by termites and flickers illustrates this type of behavior.

F. Through finding, fitting, and constructive activity in combination, that is, the construction of a niche in an already existent cavity.

  1. When endogenetic material is used for construction of the niche. This type of be-

havior is illustrated by edible swifts (edible nest swifts).

2. When both endogenetic and exogenetic materials are used. This type of shelter construction occurs for chimney swifts and still occurs to some extent for "esculent" swifts (Loeser 1940).

3. When only exogenetic material is used.
   a. Instances in which cavity is modified as occurs for toucans.
   b. Instances in which cavity is not modified except as to contents as illustrated by the behavior of some wrens and certain mammals.

G. Through finding and fitting and construction; or construction only. Some swallows may build nests one year and select already existent cavities during another season.

Section 3. Securement of shelter according to the adaptiveness responsible for activity (based on point d, p. 000).

I. In relation to feeding.
   A. As a consequence of feeding as illustrated by the behavior of wood-boring insect larvae.
   B. As a process necessary for obtaining food. This holds true for moles and some spiders (Borradaile 1923, p. 93, 52).
   C. Points A and B combined as applies to earthworms.
   D. As a process carried out for food storage (at least in part). This holds true for certain species of ants in regard to certain rooms of nests (Wheeler 1910).
   E. As an indirect result, for example, as a secretory process. This phenomenon occurs for gall insect larvae.

II. In relation to protection and rest. This category is illustrated by the formation of aestivation niches by lung fishes.

III. In relation to both feeding and protection as applies to wood-boring larvae.

IV. In relation to reproductive drive. This adaptiveness is illustrated by nest construction as carried out by most birds.

V. In relation to feeding, protection, and reproduction. The niches of moles provide for a complex of functions.

Section 4. Methods of anchorage.
   I. Secretion.
      A. Secretion of adhesive as occurs for Stentor and snails.
      B. Secretion that assists vacuum formation for adherence by suction as occurs for snails.
      C. Use of spun fibers as occurs for some mollusks and insect larvae (Hesse 1937).
      D. Secretion of weight as occurs for giant clams (point V).
   II. Use of hooks, spines, or claws. Claws of appendages are used for anchorage by mammals

and arthropods; spines are used for anchorage by Scapholeberis (Carpenter 1928).

III. Use of suckers (Hesse 1937).
   A. A surface of an animal serves as a sucker. Use of this mechanism occurs for aquatic larvae of water penny beetles.
   B. Use of sucking organs.
      1. Developed on "limbs." This type of mechanism is used by male Dytiscus, some copepods, starfish, cephalopods, some Ranidae and Bufonidae, Hylidae, some lizards, some mammals, certain bats, primates, etc.
      2. Developed on body. This mechanism is used by fishes (Remora, Riacichthys, mouths of some catfishes) some frog tadpoles, certain annelids (leeches, Branchiobdella), flatworms (tapeworms, flukes), some diptera larvae, and May fly nymphs (Pearse 1939, Hesse 1937).

IV. Use of prehensile "organs."
   A. Prehensile body. This mechanism is used by snakes.
   B. Prehensile limbs. Use of this mechanism occurs for cephalopods and some brittle stars.
   C. Prehensile organs on limbs. This type of mechanism is used by chameleons, marsupials, primates, etc. (Hesse 1937).
   D. Tails. This mechanism is used by fishes (sea horse), chameleons, and snakes, some marsupials and certain other mammals.

V. Use of grasping organs occurs for some arthropods, certain frogs, and primates (Hesse 1937).

VI. Increase in specific gravity of body or shelter. Some fishes empty their hydrostatic organs. Some species lose their swim bladders through evolution. Some caddis-fly larvae weight their shelters (Hesse 1937).

VII. Indirect attachment by retreat from areas characterized by currents or pressure influences either physical or biological. This method of anchorage is carried out by procurement of shelter: excavation, finding and fitting, construction, etc.

VIII. Locomotion. Most fishes that live in rapids rely upon locomotion to bring about their remaining in stationary positions.

Section 5. Means of dispersal (see [1] Part F, and [5] Part B concerning movement of organisms).

[6] Relation of Activities

Organismal Units: Community, species, colony, symbiotic or commensal unit, and individual.

I. Community activity. Synecological activity. This category is based upon interspecific relations (Pearse 1939, p. 498-533).
   A. Active participation. Animals may carry out activities that directly involve or influence other species. Influence may be indirect as

when behavior is affected as a result of activities of other species. All predators are active participators during the time period in which they take prey. All individuals that locomote outside of their seclusion niches are active participants to some extent, since (1) their motion tends to attract predators, (2) in locomoting in the open, animals go towards predators at least a part of the time instead of requiring predators to go all the way in obtaining them. The fate of ants that fall into ant-lion traps serves as an example of an instance in which prey performs much of the work that leads to its being eaten.

B. Passive participation: passive members are concealed at least to a considerable degree through being more or less under cover, or by being immobile and protectively formed or colored, or through restricting time of rest to night, etc. Passive participators are usually taken only by predators especially adapted for securing them or/and in recognizing indications of their presence, as occurs for earthworms when taken by robins, and wood-inhabiting insects when taken by woodpeckers.

II. "Species-limited activity." This category is based upon intraspecific relations (Pearse 1939, p. 458-497). This category concerns activity between members of a species. It may be subdivided according to reproductive activities, etc.

III. Group and unit activities. Gregareous behavior (Allee 1931, 1938); flocking, forming into a circle for protection from wind or enemies, processes that bring about union with a symbiont or commensal, etc.

IV. Individualistic or independent activity: concerns activity of an individual in relation to itself only. Individualistic activities include cleaning the body, preening, general use of sound organs without regard to presence or absence of other individuals. Locomotion and feeding while in a seclusion niche, and insignificant reactions upon the physical environment may be included. It is not always possible to determine whether an activity pertains to only a single individual.

[7] NATURE OF BIOTIC FOOD AND SHELTER RELATIONSHIPS

Physiological bases for classification are mentioned under classification number [1]L. Further classification has been presented (Allee 1931, 1938).

I. Complexity of behavior and of relationships that occur between organisms. This category has two principal subdivisions.

A. Solitary behavior.

B. Gregareous behavior.
   1. Non-social group behavior.
   2. Sub-social behavior.
   3. Social behavior.

II. Nature and degree of dependency of organisms upon each other. Independence exists for many activities of some organisms. This holds true for the nutritive activity of many plants. Some organisms draw their food directly from other organisms: predator prey relationships and parasitism. Some organisms depend upon others for shelter or other benefits besides food: host-guest relationships and commensalism (Allee 1931, Emerson 1935, cf., 1938, Pearse 1939). Through special types of associations, some organisms make life requirements available to each other: symbiosis.

III. Accidental and causal factors that bring about associations (Allee 1931).

IV. Ecological values and detrimental effects of associations to organisms involved (Allee 1931, Pearl 1939, Park 1942).

V. Constituency of aggregations: homogeneous and heterogeneous associations, etc. (Allee 1931).

[8] EXTENT THAT ORGANISMS ARE EXPOSED

I. Community-exposed activity. "Community activity."

II. Community excluded behavior. Exclusively species, group, and/or individual behavior; that is, behavior that is successfully and at least temporarily independent of the rapid dynamic movements of other community members, although probably a result of influences of other species during evolution.

A. Through concealment (cf., Principal Ecological Activities IV).

   1. By inhabiting a seclusion niche without providing significant evidences of presence that are likely to lead to personal destruction, as occurs for most wood-inhabiting insect larvae during most of the duration of their larval stages.

   2. By evolving through evolution a protective coloration, protective form, and habits that bring about concealment.

   3. By restriction of quiescence for rest and sleep to the night, especially for those animals that rest in the open and do not possess shelters.

B. Partly concealed activity as illustrated by certain passive members which allow evidences such as odors, sounds, etc., to indicate their presence to at least one natural—not accidental—predator constituting a normal component of the same community. This type of behavior is illustrated by earthworms and many wood-inhabiting insect larvae.

   1. Fair extent of concealment as occurs for earthworms.

   2. Almost perfect concealment as illustrated by Tremex (Comstock 1930).

C. Through dominance, that is, by ability of animals to dominate possible enemies when attacked at any time including their resting period.

Ordinarily, the characteristics of exposure and concealment do not hold for any particular species throughout its life history nor necessarily for the duration of any particular life stage. Extent of exposure and concealment may vary, and exposure may alternate with concealment from time to time for any individual.

[9] METHODS EMPLOYED THAT INFLUENCE ACTIVITIES OF OTHER INDIVIDUALS. ACTIVITIES THAT LEAD TO COÖPERATION

I. Employment of attraction mechanisms. Activity that leads to coherence among organisms.
  A. Use of coherence mechanisms. Activity influences individuals within organismal units such as members of a species, family, group, commensal, or symbiotic unit. Activity leads to coherence among organisms that benefit from the activities of each other.
    1. Through passive exposure of the body or its parts. For example, exposure of color or form or both color and form.
      a. As a means of coherence of family members as occurs for antelopes and cottontail rabbits. Many species recognize members of their kind by their form and perhaps color. Special recognition marks are probably unnecessary at least in most instances.
      b. As a means of stimulating sexual impulse as illustrated by the influence of courting colors in many birds (Borradaile 1923, Pycraft 1914, Hammerton 1930).
    2. Through production of light as occurs for fireflies, some crustaceans, and certain fishes.
    3. Through provision of contact stimuli.
      a. Contact with other individuals. Contact of young animals with a parent may be a sufficient factor to account for their quiescence.
      b. Contact with product of action as occurs for some caterpillars that follow silk which is spun on paths.
    4. Through production of physical movements or vibrations.
      a. Production of sound (Warden *et al.* 1936, 1940).
        (1) By means of sound organs as illustrated by the behavior of many insects and birds.
        (2) By means of oscillatory contact with environment as illustrated by the tapping of woodpeckers.
      b. Physical contact movements with other organisms as illustrated by the mating stimulus of rainbow darters (Reeves 1907).

      c. Feeding of other individuals; occurs for ants and birds. This point may be considered a part of point b.
      d. Visual display of attractive behavior or/and production of attractive objects.
        (1) Peculiar motions. This type of behavior often involves color display as for prairie chickens and birds of paradise.
        (2) Building of bowers or nests as occurs for bower birds and wrens.
    5. Through release of chemicals; for instance, release of sex and species odors (Rau & Rau 1929).
  B. Use of interspecific fertilization mechanisms.
    1. Passive exposure of color or form or color and form. This function is provided by the petals of flowers.
    2. Release of chemicals. This mechanism is employed by plants.
  C. Adherence mechanisms. Activity that influences prey or host-food of next generation.
    1. Use of methods of attraction.
      a. Through chemical attraction as occurs for sundews.
      b. Through visual attraction as illustrated by color or color-form display of some plant insect traps and orchid-mimicking mantis (Pearse 139, p. 22).
      c. Through production of light as occurs for some deep sea fishes, especially the angler fishes (Beebe 1934).
    2. Use of trap mechanisms and separator mechanisms.
      a. Passive function of mechanisms as by way of growth and differentiation. Activities such as growth and differentiation involved in the procurement of traps are relatively slow and precede the function of traps. Passive traps such as osmotic contact apparatus (roots) and valve traps of pitcher plants do not depend upon rapid motion to fulfill their function. Movements involved in the function of active traps are relatively rapid and accompany or follow the capturing of prey. Some traps function without employment of dynamic force. Others are useful only when put to active employment. It is not justifiable to assume that nervous phenomena occur only in animal protoplasm. Some plants are capable of making use of a nervous property of protoplasm even though—so far as is known—this property has not developed in plants into specialized tissue deserving the term nervous tissue. However, such a development should be possible. It is worthy of note that the leaf parts of venus fly-traps do not close unless sense receptors receive stimulation at least

twice in rapid succession. Point (1) is not distinctly different from point (3) and point (2) is intermediate between the two extremes. Trap mechanisms that function passively are not distinctly different from traps that function by way of dynamic employment of force, and activity does not subdivide into natural categories according to whether a nervous system, intelligence, or volition are or are not involved.

(1) Traps functioning passively: (a) valve traps of pitcher plants, (b) strainers such as gill rakers of fishes, (c) glue traps of sundews, (d) osmotic contact apparatus, absorption surface traps such as root hairs.

(2) Traps functioning automatically through independent dynamic action of trap mechanisms: (a) some snare or wrapping traps; for example, certain nematocysts of coelenterates, (b) some piercing traps that may involve use of barbs; for instance, certain types of nematocysts function by means of spring or pressure mechanisms, (c) some piercing and poison traps illustrated by certain nematocysts, (d) grasping glue traps of sundews, (e) current traps as used by Vorticella.

(3) Traps functioning through remote control: (a) box traps such as mouths used to trap prey, (b) valve traps, for example, pharyngeal valves through which prey is forced in swallowing, (c) hook traps and barbed traps as illustrated ·by tongues of woodpeckers and hummingbirds, (d) glue traps as illustrated by the tongues of ant eaters, (e) sucking mechanisms such as mouths, beaks, and tongues of certain fishes (e.g., hog suckers), birds (e.g., hummingbirds), and insects (e.g., butterflies), and suckers such as sucking disks of cephalopods, (f) grasping traps such as raptorial legs as used by many insects, crustaceans, and chelate organs that function for crustaceans, arachnids, wasps, and primates, prehensile organs as illustrated by the body of boa constrictors and the proboscises of elephants, jaws usually made efficient by spines or teeth, grasping leaves as used by venus fly traps, (g) poisoning and paralyzing mechanisms such as stings as used by some wasps, (h) electrocution as employed by torpedo fish, (i) shooting projectiles: (1) as a means of incapacitation. This mechanism may

function by blinding as when employed by the ringhals or spitting cobra. (2) As a direct method of trapping. This mechanism is employed by archer fish, (j) sweep-net traps as employed by goatsuckers.

b. Active securement as through construction. This type of securement involves complex behavior and may involve secretory activity.

(1) Net traps as used by some spiders, some caddis fly larvae and humans.

(2) Pit traps as employed by ant-lion larvae and humans.

(3) Miscellaneous. Various types of traps made by man include some already listed for other animals.

3. Complexes of more than one method.

II. Repulsion. Activity having repulsive influence upon enemies. A different treatment of repulsion is given under Principal Ecological Activities IV.

A. Through exposure of the body or special parts of it.

1. "Warning" coloration (Pearse 1939, Cott 1940).

2. "Warning" mimicry. Batesian and Müllerian mimicry (Pearse 1939). Each instance of mimicry requires evidence.

B. Through release of obnoxious chemicals.

1. "Repellent odor" as provided by skunks.

2. "Repellent taste" as provided by toads and some plants.

3. Poisonous substances as provided by some species of fishes, certain frogs, and some plants such as nettles.

C. Through combination of exposure of brilliant color and release of obnoxious chemicals. This mechanism functions when Papilio and Ornithoptera caterpillars protrude osmeteria as a response to attack.

D. Through securement of cover. For example, production of ink screens by squids (see securement of shelter, classification number 5).

E. Through pretense or bluff.

1. By pretense of aggressiveness.

a. By aggressive motions including chase in some instances.

b. By bold attitudes as occurs for some caterpillars such as those of the pus moth.

2. By lethisimulation, that is, by tonic immobility as occurs for opossums, many birds, reptiles, some insects, etc.

F. Warning.

1. Through production of sound as a probable "warning" such as a bird song. A concept of force being a more primitive method of protection than pretense of aggressiveness or warning has been presented for birds

(Kendeigh 1941). A similar idea is held for snakes (Gadow 1908).

    a. By use of sound organs as occurs for rattlesnakes, dogs, and birds.

    b. By oscillatory contact with environment as illustrated by the behavior of some snakes (Gadow 1908).

  2. Through gestures. For example, chasing.

 G. Through use of trap mechanisms (see above). This category includes throwing projectiles as occurs for some primates, shooting "projectiles" as occurs for certain ants, nasuate termite soldiers (Emerson 1926, cf., 1938), certain beetles, the ringhals cobra (Hammerton 1930), and skunks. Man has acquired the same mechanism through invention of several types of instruments.

  1. Passive overpowerment of enemies by use of automatic trap mechanisms (overlaps with points 2 and 3).

  2. Indirect elimination of enemies through construction of traps.

  3. Active overpowerment through dynamic use of force.

III. Interchange of ideas. Communication. Means of stimulating or discouraging impulses in other individuals (Long 1919, Davidson 1936, Bierens de Haan 1929, Emerson 1929, Stoddard 1931).

 A. Through employment of sound symbols, for example, speech, telegraphy.

 B. Through employment of visible symbols, for instance, writing, facial expressions, gesture, smoke signals, etc.

 C. Through establishment of conditioned responses dependent upon symbols. For example, pain inflicted as punishment or offer of rewards as occurs for several primates.

 D. Through application of pressure as by pushing.

 E. Through performance of motions as when teaching by principle of imitation.

[10] ACTIVITIES MAY AFFECT PHYSICAL OR/AND BIOTIC ENVIRONMENTS OR BOTH

For example, coaction, reaction, interaction (Clements & Shelford 1939).

[11] EXTENT OF INFLUENCE UPON ENVIRONMENT

Animals may be predominant, subdominant, dominant, influent, or subinfluent. Activities may be referred to by the same adjectives (Clements & Shelford 1939).

EVOLUTION OF BEHAVIOR

Discussions that treat evolution of adaptations have been given by Clark (1914), Lull (1929), Crawford (1931), Elton (1935, 1927), Ewing (1935), Shull (1936), Kinsey (1936), Emerson (1938), Imms (1937), Park (1937, 1941), Kendeigh (1941), and others.

Structural and physiological mechanisms may passively satisfy the same requirements for some organisms that dynamic movements accomplish for others. It is not proper to consider mechanisms that are passively effective as distinctly different from activities carried out by way of dynamic behavior. The adaptiveness of a particular species characteristic to environment cannot be judged by absence of the same character in related species, since different means may satisfy the same ends. Related species may possess very different methods of adaptation to the same influence. To illustrate: one kind of organism may be adapted for self-defense by mechanically secreting a chemical that repels "enemies" which would otherwise destroy it. Other species may depend upon dynamic complex behavior that leads to the same end. It is appropriate to treat both dynamic activity and passive activity in classifications that are concerned with adaptations.

Mechanisms that are passively effective arise through growth and differentiation. Growth and differentiation and instinctive and intelligent acts are subject to environmental influence by way of elimination of the least fit. This amounts to a mechanism of environmental guidance.

Many mechanisms that are passively effective intergrade into those dependent upon use of force for effectiveness. Illustrations: consider variability among organisms in mechanisms that serve for means of dispersal, means of protection, methods of anchorage, mechanisms that serve for trapping, and means of procurement of shelter (Figs. 1-9).

There are intergradations between the types of activities involved in the securement of shelter by protoplasm from secretion of a body structure that serves as a support to one that serves as a shelter, from instances in which a secretion is used alone to those in which an endogenetic substance is combined with foreign material, to those characterized by use of only exogenetic material for construction. There are intergradations between functions of shelters from those that serve for reproduction to those that provide for food storage or protective retreat to those that serve complexes of functions. Shelter securement, an aspect of ecology and behavior, cannot be separated from growth, embryology, differentiation, metamorphosis, or physiology in a significant or comprehensive classification. For possible courses of evolution followed in evolvement of adaptations, one may refer to several charts (Figs. 1-9) that accompany this discussion. There is a strong tendency for activities to be adopted in order of their complexity. It is a natural law that also applies to psychological phenomena for an activity method or behavior trait of greater complexity to be preceded by activities of less complexity. Consider learning as it is involved in acquiring ability to play a musical instrument. It is not strange that this law—as well as the process of trial and error—should be important in both method of evolution of organisms and in thought procedure. Just what activities are rela-

tively complex or simple varies with a particular organism in regard to: (1) its type of physiological organization, (2) its structural and physiological complexity, (3) its ancestral hereditary makeup as may be judged in part through a knowledge of characteristic behavior of the taxonomic group in which the organism in question belongs, (4) its adaptations in relation to the general environment, (5) the nature and components of the habitat into which the organism (a) tends to remain or (b) is forced, (6) degree of intelligence, that is, ability to become adjusted to new situations.

The following illustrations show that behavior of organisms follows lines of least resistance. Activities are pursued that are the simplest so far as a particular organism or type of organism is concerned. The least complex methods of shelter construction that single cells can possibly employ are those which depend upon secretion (as for plant cells and protozoa in general). Whereas, the simplest methods that most birds can possibly use in making definite shelters are: (1) construction by means of excavation, (2) construction through use of exogenous material. These methods—incidentally determined through this line of reasoning—are also shown to be the original methods used by the first birds and their reptilian ancestors as borne out by palaeontology. For birds, the secretory method of the edible swift is the most specialized in contrast to its being a primitive method for Arcella. However, for swifts, the secretory method is not the most complex, since the "chimney-swift method" involves greater complexity in environmental relations and requires greater selectivity by the organism. This is an instance in which evolution is observed to proceed from a degree of complexity to a degree of less complexity and is comparable with retrogression or degeneration of structure as happens in parasites. These suggestions account for a tendency of behavior traits to be recapitulated in individuals in the same order as occurs among different organisms on the scale of phylogenetic complexity from the simplest to the most complex. Behavior traits as they evolve for a particular species and those that appear through the various taxonomic categories are comparable by analogy at least; partly, as a result of common laws that govern the development of both groups of traits. These laws are: (1) following a line of least resistance which is the easiest and most practical for the organism's equipment, and (2) complexity being led up to through development of simpler components. It is natural that simpler behavior traits are first to appear among inherited qualities since they are first to occur and prove useful. Probably, they originate and remain through mutation, orthogenesis, natural selection, etc. Gradually, more behavior traits are added, and new qualities arise as modifications of previous ones, so that a heredity-complex becomes composed of a physico-chemical basis for chains of reactions, that is, complex instinct. Finally, in some instances, complex behavior represents a peak in the recapitula-

tion of activity traits that developed in ancestors of the species. These suggestions are not in discord with the fact that at any point in evolution, certain traits, especially useless traits, may "disappear," that is, be subdued or dominated; nor do they interfere with the fact that reversion may occur. Evolution without the occurrence of intermediate steps is a likely explanation of the origins of many complex behavior traits (Goldschmidt 1940).

Evidences indicate that the behavior of molecular aggregates including protoplasm is controlled by laws which finally depend upon the characteristics of atoms (Planck 1937). The characteristics of atoms or their component parts finally depend in part upon chance (Schrödinger 1935). In other words, one finally arrives at a point where the behavior of matter is not always predictable even when environmental conditions are known, and there can be no causal explanation for first causes. If every cause were dependent upon another cause, this state of affairs would go on to infinity.

Phenomena that occur for molecular aggregates are the results of causes which in turn depend upon causes which in turn or in a sufficient number of turns depend upon the characteristics of the particles that make up matter. To date it cannot be explained in all instances why atoms behave just as they do. One cannot conceive of any factor except chance to account for first causes. In the light of modern knowledge, behavior of matter that conforms to natural laws which apply at least to molecular aggregates falls within the scope of determinism.

Evidently, matter behaves in accordance with laws that can be expressed by mathematics (Rashevsky 1938, 1940), and it appears that determinism governs the behavior of organisms with the element of chance entering in when explanations of first causes are desired. This would hold not only for ordinary behavior but for changes that occur in matter whether it be changes involved as uranium divides into radium and other substances, or as simple organisms become complex colonial units, or as mutations take place in the genes of chromosomes.

If evolution occurs in accordance with laws, that is—by way of determinism—then life would probably always develop in the same manner under definite complexes of conditions whether it be on another planet exactly like that of the earth or whether it be on two or more separate parts of the same planet. That is to say, this principle should apply to the evolution of life on different parts of the earth where environmental conditions are similar and where organisms are sufficiently separated to prevent their inbreeding. Determinism evidently plays an important part in evolution, and genetic relationship is only one of the factors that accounts for the similarity of structure and behavior among different organisms.

The simplest organisms probably gave rise to metazoa and metaphyta in many distinct instances and so on up the evolutionary scale. Convergence and parallelism and straight-line evolution have oc-

curred much more commonly than is indicated by evolution "trees." This holds true for the evolution of behavior; and convergence, parallelism, and straight line evolution should also be important in bringing about the various structures and forms as we see them in different species.

The mole life form represents one of the adaptive radiations that mammals might take when they take to the ground to live. Different species of insectivores that took to mole habits in the remote past should develop into a "mole." That mole environment is capable of "moulding" animals as a result of natural selection influences into the mole type, is proved by the existence of a marsupial "mole." If the marsupial mole had been a generalized Australian insectivore instead of a marsupial at the beginning of its underground life, it would now be arbitrarily included in a mole, shrew, or mole-shrew "family." Therefore, criteria upon which phyla, orders, etc., are based may be largely arbitrary and artificial.

The same principles are illustrated by the development of similar organs such as cephalopod and vertebrate eyes. If natural laws can bring about the development of such similar structures as cephalopod and vertebrate eyes without depending upon genetic relationships, the same laws can bring about the same close similarity among organisms. It should not be possible for taxonomists to know how much genetic relationship accounts for similarity in structure except for individuals of subspecies and species that interbreed or can interbreed (Dobzhansky 1937). However, the following rule should hold: the more similar organisms are, the greater the probability that their similarity is to be accounted for in part by genetic relationship, especially recent relationship. This probability might amount to 100 per cent for animals that interbreed regularly.

For evidences that some taxonomic categories represent artificial concepts in part, see Kinsey (1936) and Huxley (1940).

For evidences that evolution tends to occur along straight lines perhaps as often as it tends to continue by branching, see Kinsey (1936), Neumayer & Hyatt (cf., Locy 1908, p. 355), and discussions on orthogenesis (Eimer, etc., cf., Lull 1929).

Ideas similar to those here expressed have appeared in previous writings (Gadow, cf., Jordan & Kellogg 1922, p. 205). The principal fault of the evolution concept that holds prominence is that it does not recognize the possibility that several mechanisms may be about equally important. In other words, most theories that concern evolution have considered one or two principles as important and disregarded others almost entirely. According to one theory, the importance of natural selection is overemphasized (Willis 1940, Darwin, cf., Lull 1929). In another, the importance of divergent mutation is exaggerated (Willis 1940); whereas the importance of genetic relationship is underestimated by Gadow. Jordan & Kellogg (1922) strike closely to a middle ground that recognizes the importance of several principles.

Taxonomic parallelisms are recognized by Seitz (1930, vol. 14, p. 387).

This discussion is an attack upon the dogmatic assumption (1) that evolution of all taxonomic groups depends entirely or almost entirely upon divergence so that genetic relationships may be diagrammed in the form of a tree, (2) that similarity signifies genetic relationship, especially when taxonomic features are not adaptations to environmental influences.

There is sufficient reason to believe that when protoplasm reaches a certain age under conditions within definite limitations, specific changes (mutations and gradual variations) tend to take place to lead evolution in one or two or rarely a few (but never an unlimited number) particular directions. This reasoning is based upon (1) a philosophy of "determinism" (laws of cause and effect perhaps built partly upon chance in final analysis) supported by what is known of physical and chemical laws as they are known to function, (2) evidences of orthogenesis (Lull 1929), (3) the fact that in many instances resemblance between different types of organisms are too perfect to be accounted for by chance or by the benefits of mimicry. See illustrations of similarities between types of butterflies (Punnett 1915). (4) Universal processes. Some processes appear to be occurring throughout groups of organisms independently of close genetic relationship. The primitive condition of spermatophyte and fern leaves is supposedly the uncut and simple leaf type. It is easy to observe that simple leaves tend to become compound and doubly compound leaves tend to become triply compound (now in the process of occurring in honey locusts), and simple leaves tend to become serrated and incut. Papaw, spicebush, and magnolias are among the few plants that have retained a primitive condition for the most part. Even some papaw leaves are incut.

As a result of the function of natural forces upon molecules and molecular aggregates, parallelism should be a common phenomenon. The extent to which genetic relationship exists between species that comes about through parallelism can probably not be determined; that is to say, there is no criterion for determination to what proportion genetic relationship, parallelism, and convergence function in bringing about the nature of structures and behavior of species within a genus, genera within a family, etc. However, the higher the category, that is, the greater the total similarity, the greater the probability that genetic relationship is an important factor in accounting for similarities.

The extent that parallelism plays in bringing about similarities among organisms and how much divergent evolution plays in bringing about differences cannot be answered without basing judgment upon whether natural changes come about haphazardly or function mainly in accordance with laws. The answer to this question falls upon organic chemistry, physics, and mathematics, at least as much as upon biology.

The unit of measurement that should serve for judgment of the amount of difference in structure and behavior that can occur among members within a single species is the amount observable for the sexes of sexually dimorphic species and perhaps also for the alternate generations of metagenetic species and perhaps for those which differ in type in different seasons. Examples of sexual dimorphism serve as proof for the previous statement. The limitations to structural and behavior variations within species are not rigid and may be scarcely limited. Consider the amount of variation within certain species of moths (Lutz 1918, p. 18), Lernaea, Bonellia (Borradaile 1923, p. 171, 173), and Coccidae (Comstock 1930, p. 441). Probably the total extent of similarity possible between remotely related species should be as great in magnitude as the amount of difference that can occur within a species. At least, this is regarded as true according to present taxonomic standards. Structures should not constitute a problem in addition to that of behavior since they come about as a result of the behavior of protoplasm.

Conclusion. Divergence, parallelism, and convergence all function in accordance with natural laws to determine the nature of structures and behavior. As a result, genetic relationships are likely to be obscured in many if not most instances. Taxonomy is as important as ever, but all of the taxonomic categories except individuals—and perhaps species—cannot be regarded as more than artificialities. The one criterion which ecology can recognize to distinguish between species is whether or not members of one type regularly interbreed with another type to produce fertile offspring; that is, human discrimination between species depends upon the species reaction to or recognition of its own kind. This type of reaction is a special kind of coaction. The criterion is acceptable to Dobzhansky (1937). Ideas expressed in this discussion are not in disagreement with those of Goldschmidt (1938, 1940).

SIGNIFICANCE OF SYNCHRONIZATION OF ACTIVITIES WITH DAY AND NIGHT

Probable advantages of nocturnalism and diurnalism have been presented by several authors (Clark 1914, Crawford 1931, 1934, Park 1939, 1940). These advantages are believed to account for natural selection of mechanisms that limit occurrence of activities to appropriate time-communities. Theoretical discussions of this problem have also been given by Vestal (1914), Kennedy (1928), Pearse (1934) and others. A summary of the likely survival value that nocturnal activity has in relation to relative humidity, temperature, and evaporation rate, and other factors has been presented by Park (1939, 1940).

Limitation of activities to appropriate time-communities may be due to one or more advantages provided by special environmental factor complexes: (1) availability of food [(a) There is much evidence that community activity of predators is greatest during periods in which their prey is also most active.

Such a relation is analogous to the fact that an animal's most important competitors are usually members of its own and closely related species. There are exceptions to the rule (Pearse 1939, p. 499). (b) A theory that has no evidence for support except for few animals holds that predators have adapted themselves to be active in a period during which their prey is at rest and incapable of preventing attack. In both instances, it is held that advantages for securement of food are sufficiently great to bring about confinement of predation within appropriate time-communities characterized by availability of food]. (2) Opportunity for evasion of enemies (Elton 1935, p. 88). Reasoning dictates that nocturnalism of the crayfish, *Cambarus virilis,* has come about through natural selection of behavior that leads to avoidance of predators. This species of crayfish is a plant feeder and scavenger, so its nocturnalism cannot be accounted for as an adaptation for securement of food. (3) Opportunity for elimination of competition of other species for food (Vestal 1914) or shelter (Elton 1935, p. 83-84; Willey 1904, cf., Park 1940, p. 500). (4) Availability of illumination that permits the best possible visibility. Most birds of the temperate zones are diurnal in relation to this influence. (5) Opportunity to avoid exposure to high temperatures (Elton 135, p. 88; Pearse 1939, p. 426). (6) Opportunity for removal from air having a high evaporative power (Park 1938, p. 209). (7) Opportunity for transfer to a secondary host (Elton 1935, p. 87). (8) It is not improbable that a complex of influences already mentioned accounts for the survival value of nocturnalism and diurnalism for many species of animals; for example, both points 5 and 6 are of advantage to certain desert animals.

It is worthwhile to give theoretical consideration to certain of the advantages gained by limitation of activities to day and night. What animals are nocturnal as a consequence of adaptation to times at which food is available and predators are avoidable can be determined only through application of logic to facts secured by observation and experimentation. Sufficient information has not been obtained in order to make application of reasoning to this problem possible for most of the known animal species.

It is probable that most North American species of owls became nocturnal as a result of increased availability of prey such as mice that had already become objects of instinctive attack. There are a limited number of environmental influences that determine the preservation of tendencies of animals to be active in appropriate time-communities. Such influences are listed at the beginning of this chapter. Elimination of factors not likely to have influenced timing of food securement for owls leaves only points 1 and 2 as possible explanations for development of their nocturnalism. Since owls are as capable of self-defense as most other diurnal birds, and since owls probably have not had any specific or important diurnal enemies, only point 1 remains as a likely explanation for nocturnalism of

owls. However, it is also possible that adaptation for night vision preceded and determined adoption of nocturnal behavior.

Not much information has been obtained concerning the extent that carnivorous animals prey upon sleeping or quiescent animals (Elton 1935, p. 83-100). Behavior of owls illustrates that sleeping and quiescent animals are more likely than are active animals to be overlooked by predators (Eaton 1920, part 2, p. 116). The examination of stomach contents of many birds by the United States Biological Survey reveals that of seven species of owls studied extensively, only one species—the great horned owl—commonly preys upon sleeping animals. The species studied were: the barn, long-eared, short-eared, barred, saw-whet, screech, and great horned owls. The great horned owl normally preys upon skunks, rabbits, mice, and muskrats. The screech owl feeds upon mice and insects. The food of the saw-whet owl consist almost exclusively of mice and insects. For the remaining species, 60 to 95 per cent of their food consists of mice, and 5 to 12 per cent consists of small birds. The barred owl and other large owls commonly prey upon the saw-whet owl. The barred owl is known to feed commonly upon crayfish, frogs, insects, and birds. Concerning the barred owl, Eaton (1920, p. 116) wrote: "I have known repeated instances of poultry roosting in the trees of a farmyard where these owls were hooting every night about the place without a single fowl being disturbed. About 16 per cent of their food consisted of birds. The remaining proportion consisted of mice." Similar information is available for most species of Herodiones and Caprimulgidae (Eaton 1920). The Strigidae, some of the Ardeidae, and Caprimulgidae comprise almost all of the North American birds that are active at a time when feeding upon sleeping diurnal animals would be possible.

Predation of most animals is limited to the nychthemeral period in which prey is most active. Take for example: predation by flycatchers, most feeding for the majority of warblers, wrens, shrikes, hawks, owls, eagles, herons, gulls, goatsuckers, kingfishers, mice, shrews, skunks, bats, and most predation for members of the Canidae, Felidae, and Ursidae (references: treatises on special taxonomic groups, natural histories, United Sates Government Farmers Bulletins, United States Department of the Interior Fish and Wildlife Service, and Wild Life Review).

Florsheim (1906) states that diurnal forms are in a less alert condition at night "at which time they are quite available to nocturnal predators." Clark (1914) holds that nocturnal predaceous mammals and birds take prey when least capable of defense, in fact, "owe their nightly activity to such an ecological arrangement." These views have not been attacked. The total evidences that the writer has found to support these assumptions are as follows. A few species of animals uncover and prey upon animals that are sheltered from most possible predators. The pro-

portion of North American animals that have such specialized tendencies for securement of food can be listed in little space, and it is obvious that these animals constitute a very small proportion of the total number of species and individuals. An attempt is made to mention taxonomic groups that cover all species that possess such tendencies. Most examples include species that occur in North America. Predators that usually uncover animals while the latter are concealed in niches include: sandpipers, turnstones, towhees, oyster catchers, badgers, hogs, anteaters (Edentata), aard varks, brown creepers, most woodpeckers, nuthatches, titmice, and some species of snakes. The tendency of robins to uncover earthworms falls into this category. Squirrels, snakes, jays, and crows occasionally rob bird nests of eggs and young. Many carnivores attack poultry and stock while they are resting. Carnivores known to prey upon poultry or other farm or ranch animals include: the puma, the lynx and wild cat, leopards, tigers, lions, foxes, wolves, weasels, and hawks. Coyotes and wolves usually do not attack poultry or stock except during periods in which food is scarce as in winter. The extent that most carnivores prey upon sleeping animals especially in the wild has not been discovered. Confinement and domestication have placed domestic animals at a disadvantage so far as vigor in fighting and possibility of escape from enemies is concerned; and, unless it can be shown that animals which attack sleeping farm animals also make similar attacks upon wild species, such a food relationship has little ecological significance.

Change from either diurnalism or arhythmicity to nocturnalism should not always be a successful means of escape from predators. It appears that specific predators can occasionally adapt their own time for activity to time of activity of their original prey in part as a consequence of increase in sensitivity of certain of their sense organs as evolution progresses.

On the other hand, as species become nocturnal, their predators do not always adopt special nocturnal adaptations sufficiently effective to make nocturnal hunting of original food possible. The difficulty involved in development of organs that are hypersensitive to particular types of stimuli may be responsible for retention of diurnalism for many carnivores such as hawks. Hypersensitive senses referred to include: hypersensitivity to light such as occurs for owls (Vanderplanck 1934, cf., Park 1940, Dice 1942, personal communication) and most members of the Felidae, hypersensitivity to sound-producing vibrations as occurs for bats (Griffin & Galambos 1940), and hypersensitivity of the olfactory sense as developed in many members of the Canidae including blood hounds. It is believed that all of the carnivores including the Canidae also rely upon sight in order to capture their prey. Personal observations indicate that night-jars rely upon sight for capture of food and that bats may rely partly upon vision for the same function. Evidently, sight has become useless only for subterranean animals such as moles, cave

animals, and for most of those animals that live in the deep sea (Pearse 1938, Hesse 1937).

It follows that most vertebrates—whether nocturnal or diurnal—rely upon sight for securement of food. It appears to be evident also that nocturnal predators are usually attracted by motion of prey instead of the latter's color and shape. Motion also tends to be the important factor that attracts diurnal predators (Borradaile 1923, p. 87). Protective coloration may also be of assistance even to animals that are exposed at night (Verrill 1897, cf., Park 1940). After predators are attracted to moving objects that represent possible food, the prey is followed or forgotten according to whether or not its size, form, and color are in accord with what represents food to a species—as determined by instinct or past experience of particular individuals. These considerations make it apparent why many diurnal animals have little need of protective resemblance to surroundings.

Vestal (1914) suggests that there are several types of characters to which animals may become adapted "so as to be removed from competition for food . . . one of which is biographical—permitting adaptation of life cycles to favorable seasons, feeding to particular times of day, etc." Pearse (1934) looks upon such an idea with approval. Elton (1927) and Park (1931, p. 709, 1937, p. 16) indicate that nocturnal and diurnal faunas constitute associations ("communities") that are quite separate from each other.

Nocturnalism is probably no more often an adaptation to securement of food than it is an adaptation for escape from predators and other detrimental influences. Darwin's logic concerning survival of the fittest animals involves both struggle for food and struggle against being eaten. So far as has been determined, both of these factors are equally important in guidance of evolutionary trends. In most instances diurnalism is more likely to be an adaptation for securement of food than an adaptation for escape from predators, since diurnal predation does not require as great a specialization of sense organs of predators as is required by nocturnal predation. That nocturnal animals may adopt diurnalism should be possible; however, no instances of secondary turn to diurnalism are definitely known.

THE PROBLEM OF PROTECTIVE COLORATION AND FORM

The fact that most male birds and butterflies are brilliantly colored is not to the disadvantage of their species, because during their period of greatest activity, if one of a species is to be taken by a predator, it will more likely be a male than a female. The disadvantage of brilliant color to male birds is not so great that they cannot usually hold their own long enough to take part in reproducing their kind. Birds obtain protection by being alert, by employing the partial tonic immobility mechanism during first indications of danger, by communicating a call to others that results in quiescence and in part, by

maintaining a sufficiently high reproductive rate for their species to outlive misfortunes of individuals. Conspicuousness of diurnal animals cannot be used as an argument against protectiveness of "concealing coloration and form." The important point to remember is that the nocturnal animals which do not tend to conceal themselves by taking to shelter are protected by concealing coloration during the day, that is, during the sleeping period when they would not be very capable of self-defense if attacked by larger predators. According to the writer's knowledge, not a single nocturnal moth, nocturnal bird, or nocturnal mammal shows conspicuous coloration while in its resting poise during the day, and the relatively few conspicuously colored nocturnal animals such as certain salamanders and lizards obtain concealment under shelter during the daylight period. Exceptions such as the gila monster are few; they are poisonous, or are adapted for protection in some other manner. It is worth remembering that the only brilliantly colored moths (Catocala sp., Uraniidae, Zygaenidae, and similar species, Seitz 1930) are diurnal fliers and rest in such a manner as to cover their brilliant colors. Fishes can afford to be brilliantly colored in part because their visual sense does not become useless during the day. Most conspicuous fishes live in a brilliantly colored environment such as is offered by coral reefs, or are poisonous, or remain motionless among stones most of the day. Examples of the latter type have special structural adaptations for living in rapid currents.

Evidence has been offered in a previous chapter that nocturnal animals ordinarily do not attack resting prey. Other evidences indicate that most diurnal animals with the exception of several already mentioned do not commonly attack nocturnal animals. Very few species are known to uncover animals that are under shelters. These have been listed. Of those animals that are exposed during the day while at rest, most are protectively colored and none are brightly colored. Of those day-quiescent animals that are not protectively colored, other protective mechanisms that are of less common occurrence for many groups of animals replace protective resemblance and serve as its equivalent. There is no evidence in ecological literature to indicate that any animals which appear to have a well-developed resemblance to their surroundings in conjunction with quiescence are preyed upon except possibly in rare instances. On the other hand, there is much experimental evidence that animals which are colored or both colored and formed like their natural surroundings are seldom attacked by predators when both protectively colored and more conspicuous foods are available at the same time (Pearse 1939, p. 21, Cott 1940). It is probable that nocturnal animals are protected during the day from diurnal predators by being protectively colored and shaped or by being concealed under shelters to about the same degree on the whole that diurnal forms are concealed at night from nocturnal predators as a result of reduced light intensity. The extent that

nocturnal and diurnal communities are protected from each other balances and illustrates one of the "balances of nature."

IMPORTANCE OF RECOGNIZING TYPES OF BEHAVIOR

IMPORTANCE OF ACTIVITY CLASSIFICATIONS TO STUDENTS OF BEHAVIOR

A comprehensive classification of behavior should provide a synopsis of all activities. Books on "Animal Behavior" that have appeared thus far do not cover all of the available categories of importance that pertain to the field treated, so their titles are misleading. Some treatises entitled "Psychology" do not limit their analysis of behavior to activities that involve mental phenomena. They are valuable to students of physiology and behavior but tend to be overlooked by students who are particularly interested in the behavior of lower organisms. General treatises on behavior have not indicated what topics they omit from consideration so as to indicate what remains to be determined through new experimentations or by dependence upon separate writings already published.

In general treatises on animal behavior, topics covered are usually fragmentary, and many topics essential to comprehensive knowledge are omitted. An exception to this rule is offered by Warden, Jenkins & Warner (1935, 1936, 1940).

General treatises as a rule do not present several ecological aspects of behavior, whereas there are at least eleven important standpoints that serve as a basis for comparison and evaluation of ecological activities.

Comprehensive ecological texts tend to treat behavior incidentally. They distribute considerations of behavior among such topics as autecology, synecology, distribution, and parasitology, so that organization of activities is not apparent. Such a plan of organization is essential for the presentation of general ecology, and a recognition of this feature of general ecology is not a criticism.

Classification outlines of many categories of behavior have been presented. Examples are offered by the following: adaptations (Galloway 1913); tropisms (Loeb 1918; Fraenkel & Gunn 1940); group activities and biotic activities that concern food and shelter relationships (Allee 1931, 1938); timing of activities (Park 1937); reactions or responses (Loeb 1918; Shelford 1913, 1914b; Warden, Jenkins & Warner 1935-1940; Kühn cf., Fraenkel & Gunn 1940); and bird migrations (Peterson 1940-1941). Other references to original classifications are made in connection with Behavior of Organisms. Most of the condensed classifications of particular classes of behavior offered to date omit important topics or are too fragmentary to be very useful to students of behavior.

It may not be clear to students that such treatises as "Orientation of Animals" (Fraenkel & Gunn 1940)

omit certain aspects of orientation unless reference is made either to a comprehensive classification of activity or to special reviews. Topics not covered by Fraenkel & Gunn have been mentioned by Allee (1941).

"Failure to recognize the relative importance of the different activities is in part responsible for the general unorganized state of our knowledge" (Shelford 1937, p. 32).

When behavior categories are subdivided, different adaptations that meet similar ends may be compared in such a manner as to illustrate parallelism, convergence, and adaptive radiation. Primitive types of activities that exist at present for some organisms often represent stages through which other activities are reached by way of evolution. A classification of behavior shows that many physiological phenomena are equivalent to and perfectly comparable with dynamic behavior of other organisms. Growth and many other passive or automatic physiological processes belong to the field of behavior in many instances.

A classification clarifies concepts. In the preface of Fraenkel & Gunn (1940) the authors state that "the object of this book is to give an account of those reactions of animals which used to be called tropisms." There is no reason to drop the term tropism. The fact that Fraenkel & Gunn make such a statement indicates that there is unwarranted confusion not only in terminology but in the concreteness of concepts.

It is unfortunate that confusion exists in regard to the meanings of some important terms such as instinct and tropism. The variety of meanings attributed to these words is beyond justification. Instinct and tropism can change in meaning within definite limits only. Their elimination only creates necessity for other new terms to replace them. Unnecessary introduction of new terms does not help the concept situation since all new terms that can be defined only by complex qualifications (see glossary) are likely to go through stages of misunderstanding and consequent misuse. It is necessary that the significance of terms be illustrated and explained in order to prevent further delusion and uncertainty in the understanding of the important concepts they represent. Misuse of terms indicates that important concepts have not been formed that should be a part of common knowledge. Some authors have held that physico-chemical laws cannot explain those actions which are guided by desires. As a result, Loeb has received undeserved criticism. Careless thinking that results in unfair criticism ought to be pointed out when possible—in part—to safeguard thought processes of students.

A classification of activities provides opportunities to mention misunderstandings that have developed concerning the functions of structures such as the opinion that Paramecium is—to some extent—protected from Didinium by means of trichocysts.

It is possible to permit a view of many aspects of a subject to be perplexing. This point may be illus-

trated by structure as well as behavior. In some instances taxonomy must rely upon the criterion of wing venation or structure of genitalia. In other instances the nature of wing venation or structure of genitalia cannot serve in the least to show relationships. Size, shape, color, length, and width of structures and of whole organisms, behavior, and physiological characteristics are important to various extents according to the type of organism that is to be classified. If one attempts to learn all of the various criteria that taxonomists employ to classify organisms, taxonomy itself appears to be in a muddle. Nevertheless, various criteria are important in making taxonomic evaluations and are essential to the clarification of taxonomic relationships (Huxley 1940).

All of the points in a comprehensive classification of behavior cannot be used to classify the activities of all organisms because many organisms do not possess particular features of action. This is comparable to the fact that all points that may possibly apply to the taxonomy of organisms cannot apply to all types of organisms. Naturally, responses to images are not involved in the behavior of protozoa. By analogy, the criterion of wing venation cannot be applied to the taxonomy of sponges. The same combination of criteria cannot usually be employed to evaluate the behavior of different kinds of organisms.

Behavior of some organisms may be analyzed in greater detail than the behavior of other organisms as a result of differences in complexity. By analogy, the possibilities of considering different structures for taxonomic classification of species and genera of amoebae are far less than the possibilities for considering the differences of structure among species and genera of crayfishes.

All activities do not have equivalents. Some taxonomic categories for particular groups of organisms are not subdivided at present. For example, some orders are not divisible into families. They do not need to be subdivided unless new equivalent types of organisms are discovered. By analogy, some types of activities do not lend themselves to subdivision at present.

The original and fundamental problem of adaptation is borne by protoplasm—not by organisms. Organisms are units of matter that represent protoplasm in the various forms that it may take.

Protoplasm has become adapted to catch food by forming valves in some forms such as pitcher plants and by forming trap mechanisms that function as a consequence of rapid movement in certain other organisms. Both types of adaptations are brought about via movement—that is, dynamic behavior—of protoplasm. Rapid dynamic movements of parts of organisms represent a type of behavior that is on a higher level of evolutionary advancement than embryonic and post-embryonic growth and differentiation movements. Weiss (1939) has made it clear that post-embryonic growth and differentiation movements are not essentially different from growth and differentiation movements of embryos. He has also emphasized that embryonic and post-embryonic growth and differentiation movements are regulated by responses to stimuli and by endogenous influences that also serve as regulators of more rapid dynamic behavior of whole organisms. A strict line of separation cannot be drawn between behavior and embryology or physiology. In this outline an attempt is made to restrict behavior principally to post-embryonic activities and to those movements that have a direct relation to the external environment.

This treatise could be properly entitled: Ecological Classification of the Dynamic Behavior of Protoplasm. The term *Protoplasm* may be replaced by *Organisms* since organisms represent protoplasm.

Summary: It is better to have a fairly comprehensive condensed classification of activities available to students of behavior than to have none. An excellent classification should come eventually. The outline entitled Behavior of Organisms is in the process of expansion.

To produce work that brings criticism stimulates both thinking and investigation that in turn bring about improvement of that which is attacked. This is one aim of publication.

A general survey of available knowledge of animal activities can be summarized and organized in a manner that encourages comparison of activities that serve the same purposes or needs.

To attempt to grasp the whole of animal behavior by covering most of the important treatises on animal behavior leaves comprehension of the subject in an unorganized state. A classification places knowledge on a scientific level. One of the important functions of science is the organizing of knowledge.

It is not implied that general treatises should cover every possible topic in detail. However, literary works on behavior should state what topics are not covered by their titles when the latter do not accurately designate what material is treated. The scientific attitude dictates that titles should not refer to more than what is covered. When it is pointed out that certain aspects of behavior are scarcely treated in the literature, it becomes apparent what fields offer the greatest opportunities for research.

IMPORTANCE OF DISTINGUISHING BETWEEN THE KINDS OF ACTIVITIES THAT ARE OBSERVED OR RECORDED

The time-distribution of relative degrees of quiescence and general activity through day and night usually has purely physiological significance. Many animals are active in some way or another through a considerable portion of both day and night. Sleep is a type of activity (restful activity) and for some animals involves sleep movements, which indicates that mere movement is not of ecological significance. This point is illustrated by fishes and humans.

Time-records of nychthemeral or seasonal movements are not ecologically significant except when such facts as the following are determined: (1) Normal place or places in which activity occurs, that is,

nature of the environment in which movement takes place; (2) adaptive accomplishments of particular types of movements; (3) nature of movement; whether accomplished passively or actively, and whether accomplished by means of appendages or other mechanisms.

Community activity involves procurement of food and exposure to enemies and is correlated with movement of animals through their habitats. Therefore, for purposes of measurement—when opportunity for distractions that might influence reproductive or parental tendencies is eliminated—community activity can be represented by locomotion outside of niches for animals that do not wait for food to come to them.

It is to be expected that the usual degree of overlap should exist between community and species activity as normally lies between synecology and autecology. Reproductive activity includes courtship and breeding behavior and consists largely of species activity. When birds obtain food for their young, community activity is involved and family activities may alternate with or be superimposed upon community activities. In all instances, special recording devices and direct observation are useful in discovering the nature of individualistic, family, and community activities and in separating activities as to types. By comparing locomotor activity curves of an animal when solitary and when paired both in and out of the breeding season, and subtracting differences, a curve of locomotor activity having to do with courtship and breeding can be derived. Apparatus has been used successfully in the field to record reproductive and community activities (references noted below in connection with technical difficulties).

Personal or individualistic behavior includes sleep and semi-sleep movements, movements involved in body cleaning, preening in birds, and spontaneous use of sound organs. It is not desirable to allow the latter type of activity to be registered as locomotor activity, nor to confuse the two in a general activity curve. Activity curves are not comparable on a similar basis when dependent upon criteria belonging to different classes of behavior.

The occurrence of a discrepancy as a result of using an autecological behavior trait for measuring community activity is illustrated by the following examples based upon personal observations. Mockingbirds often sing through most of moonlight nights. During late April and during May (Urbana, Illinois) robins commonly sing from 2:30 A.M. until shortly after sunrise. Their singing through the day is generally limited to brief or intermittent periods and usually is prominent during evenings. Rainy days bring about modified behavior and are not considered in connection with ordinary activity. The robin's call notes are prominent at twilight and are often associated with a group activity such as flocking. These facts do not indicate that the nocturnal activity of mockingbirds and robins has any significance except as an autecological behavior trait. Ornithologists

continue to regard these birds as being almost entirely confined to the diurnal time-community even though records of song and call notes through the day-night cycle would often show their activity to be predominantly crepuscular or/and nocturnal. Their voice curve does not correspond to their locomotor curve as we know it to be, and it becomes evident that the time at which sound is produced by special organs of animals does not indicate the time at which their community activity occurs except when sound production can be shown for specific instances to be associated with activities of other community members.

Crayfishes often move about in their seclusion niches and clean various parts of their structure during the day. They lose their nychthemeral locomotor rhythm while mating. These individualistic and breeding behavior characteristics do not alter the fact that the activities of the virilis crayfish that concern its relationship to various members of the community occur almost completely within the nocturnal period.

Some species of animals become predominantly nocturnal temporarily for breeding activities in a way that is analogous to temporary terrestrialism of sea turtles during periods of oviposition. For the adults of some species, for example, may-flies and mouthless moths, activity is restricted entirely to the nocturnal period for reproductive functions only. In certain species of turtles, community activity may be mainly diurnal, but activities that have to do with oviposition are nocturnal. It appears that for some species of animals, only one of the reproductive activities occurs under the nocturnal realm while other activities except purely physiological processes occur during the day or during both day and night. It is not unlikely that the reproductive drive will prove to be an important factor responsible for pronounced nocturnalism in some kinds of animals and for temporary increase in diurnalism of others as holds for most crayfishes during mating. Feeding at night may be a secondary and temporary phenomenon that secondarily accompanies a special time for reproductive activity among some kinds of animals such as most sphynx moths. Feeding is limited to a considerable extent to their larval period. Therefore, consideration of time of feeding for many species must involve the larval stages.

A pond at 1003 West Nevada Street, Urbana, provided personal opportunities to observe activities of toads during a period of two years. Casual observations suggest that locomotor and calling activities of male toads are not predominantly nocturnal before or after the breeding season. Nor is bodily activity restricted to night during the breeding season as has been well shown through carefully conducted research (Higginbotham 1939). Also, in a number of instances, males were heard to sing through the morning until after noon and again before sunset. Only adults came to water (all of the males copulated when offered mates and all of the females laid fertile eggs).

Three toads were observed to eat ants while exposed to the full rays of the sun at midday in middle July, 1940. During dry periods in summer, the toads covered themselves with soil and usually remained in it at night as well as during the day. A long white string attached to a hind leg of each individual permitted their positions to be noted. Night proved to be perhaps no more important than moisture (and perhaps other factors) in regulating time of activity. The toads would remain in the soil through many dry days and nights and emerge during rains whether rain fell during day or night. Preponderance of nocturnal activity was not to be observed before or after the breeding season. Usually, the toads moved about in the evening only until they secured an aquatic habitat. The females remained quiet after reaching water. The only activity of males was singing unless a female was noticed. When a female was observed, it was pursued. During mating, nychthemeral rhythmic tendencies were reduced or lost. Copulation continued during both night and day—mostly in water, but also continued for copulating pairs when they were placed in terrestrial niches.

Two points deserve emphasis. (1) Vocal utterance is more likely to be concerned with autecological activity—reproductive activity in particular—than with community activity, probably rarely with the latter as should be possible in instances characterized by associations of different species for mutual or cooperative interests. For example, sounds made by some species may have value to other species for such partnerships as occur between ostriches and zebras; giraffes and elephants (Roosevelt & Heller 1914; Borradaile 1923, p. 109; Allee 1931, p. 30). Evidence that vocal utterances excite the attention of predators is probably meager if it exists in any quantity. Direct observation of time of feeding shows that an animal's taking of food—its principal community activity—tends to occur independently of vocal activity and may occur in a different time period than that in which vocal utterances are prominent. (2) It is important to be concerned with the ecological nature of immature animals at least as much as with mature individuals, because at any given time most communities usually consist of more immature individuals than adults (Darwin's evidence of overproduction). Analysis of activity of immature individuals and adults when not studied during the breeding period should—on the whole—contribute a worthwhile picture to a knowledge of the synecology of various species. Probably, this information would come nearer to representing truth than the knowledge which can be derived from studies of adult activity alone when recordings are based largely upon activities directly or indirectly associated with reproduction; since, in the behavior of the immature, the reproductive influence is ruled out. For the picture to be complete, activity of adults during the breeding period would need to be studied also.

It should be kept in mind that the significance of an animal's activity varies according to whether it is viewed from an autecological or synecological viewpoint. The only consequence to the flight of Saturniid moths and May-flies so far as species adaptation is concerned is the finding of mates and laying of eggs in a suitable habitat. Their activity centers entirely around reproduction (reproductive activity). A drive for food has been eliminated from the behavior of adults. However, from the standpoint of the community, such animals are to be included with the wheels turning in the community machine, since their flight excites attack by nocturnal predators to a greater extent than does quiescence. A classification of activities includes the following possibilities. So far as the autecology of a species is concerned, certain activities may involve or tend to influence other species in communities (community activity) or may be dependent upon its own species only (species behavior). Certain activities of an individual may pertain to itself only (individualistic behavior).

So far as synecology is concerned, animals may take part actively or passively in community dynamics, or they may be excluded from the influences of the dynamic activities of other community members. Exclusion does not tend to apply to complete life histories of any species. It usually holds only for particular life stages of particular species such as wood-boring lepidoptera. The extent of exclusion varies among different species since animals may be entirely exposed to community dynamics, or they may be more or less successfully hidden from predators by retreat or by possession of both protective coloration and a tendency to remain motionless, or by restricting exposure during rest to night when natural light intensity is reduced to its minimum intensity.

Apparatus can be relied upon to automatically record the time at which a few principal types of activity such as locomotion, rest, incubation and feeding occur for a great variety of animals when appropriate controls are employed.

It serves to eliminate error in analysis of activity when each type of activity is measured and studied as separately as possible from every other type. After different kinds of behavior have been studied as to their particular time of occurrence, it becomes possible to discover what relation each activity has to other types. After different activities are studied, an attempt to determine interrelationships between different kinds should be attempted. One result should be an understanding of how different activities are integrated.

To observe, measure, and summarize at random all of the activities that can be observed gives unorganized accounts of behavior.

DISCREPANCIES ENCOUNTERED IN DIRECT MEASUREMENT OF ACTIVITIES

DISCREPANCIES CAUSED BY THE LOW RATE OF SPEED OF 24-HOUR KYMOGRAPH DRUMS WHEN USED IN CONNECTION WITH DIRECT RECORDERS

Certain limitations in direct methods of measuring activity and discrepancies that tend to occur on 24-

hour kymograph drums have been mentioned (Stewart 1898, Roberts 1940, Spoor 1941).

During periods of an animal's activity, opportunity is offered for overlapping of activity marks whether rate of locomotion is constant or not. Rate of locomotion is regarded as constant for accurate judgment of error since the important concern is with theoretical possibilities of error in method while all variables are constant except time at which activity occurs.

I can be observed that as a result of overlapping of activity record marks ("units") opportunity for errors of over 90 per cent are offered by the 24-hour kymograph for any quarter of a minute or for periods of longer duration. The same degree of error is possible when amount of diurnal activity is compared with that of a nocturnal period (Figs. 11, 12, 14, and 15).
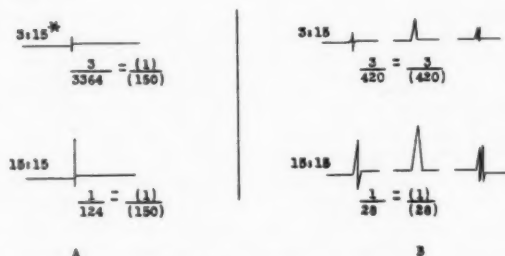
FIG. 11. Variation in value of activity record marks that appear to be of equal value on the 24-hour kymograph drum when rate of locomotion is constant. *The ratio indicates the number of seconds of activity compared to the number of seconds covered during movement of the kymograph paper. The fractions not enclosed in parentheses are the proportions of an inch that should be represented on the record for the time covered (15 seconds). The fractions in parentheses are the actual proportions of an inch consumed, as shown on the record by markers. The discrepancy is due to the minimum size of markers, and is eliminated by providing recording paper at a relatively rapid rate as illustrated in B.

A. As registered on the 24-hour kymograph drum moving recording paper at a rate of 1.07 inches per hour. B. As registered on the chronograph providing 8¼ to 8½ inches of recording paper per hour. In section B, there are three examples taken from an infinite number of possibilities.

The horizontal distance covered by a marker per hour on a conventional drum is about 1.07 inches. Practically 1/3364 of an inch is covered per second. 1/3364 of an inch is about twenty times narrower than the finest line that can be drawn distinctly by practical markers. 150 lines to the inch requires a clear space on each side of each line, or a total of 301 spaces per inch. The same limitation is encountered in printing. A fine photographic print is commonly made according to a 150 screen. It is concluded that although the maximum number of distinct lines that can be drawn by a marker is from 150 to 200 to the inch, the number of activity "units" represented for the same period can amount to at least several hundred. This conclusion is supported by experimentation with fine marking pens, pencils, and wax
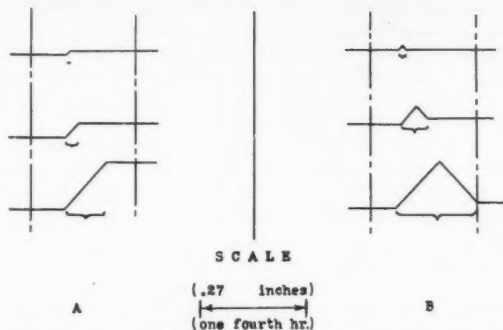
FIG. 12. Variation in values of kymograph marks which are generally counted as units of activity. They do not ordinarily represent similar durations of activity. (Width of brackets indicates the general duration of activity but does not account for short rest periods.) A is about half the value of B.

markers and by direct observations of the process of overlapping of marks during the movement of recording levers connected to crayfish. The number of marks (distinct from horizontal lines) that can possibly show is many times greater when recording paper is provided at a sufficiently rapid rate (Figs. 11, 13, 14, and 15).

Since for direct recordings, a horizontal mark represents no activity, it is appropriate to count as activity marks those which diverge definitely from the horizontal plane and those which reverse their vertical slant. It follows that an overlap is not necessarily a retrace since amount of error (overlapping) following an unrecorded rest period (which should show as a horizontal line) is the same whether an activity record mark continues to be made upwards or downwards in reference to its previous position (Fig. 13).
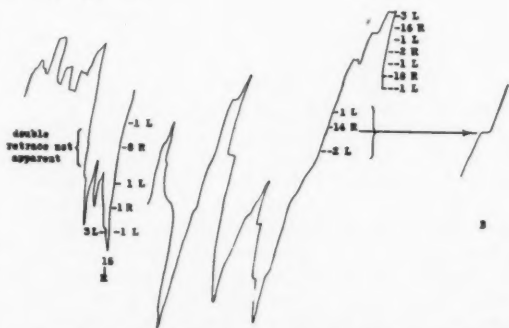
FIG. 13A. Tracings from a marking lever recording of crayfish activity on a 24-hour kymograph drum, illustrating that rest periods commonly occur without registering. A free hand drawing of this activity record was made as the original was being recorded by the crayfish. The rest periods were noted at the same time. Key (numbers indicate number of seconds): L = activity periods; R = rest periods. B. A portion of the slowly recorded curve as it would appear on a sufficiently rapid chronograph. This illustrates an overlapping of units on the 24-hour kymograph drum.
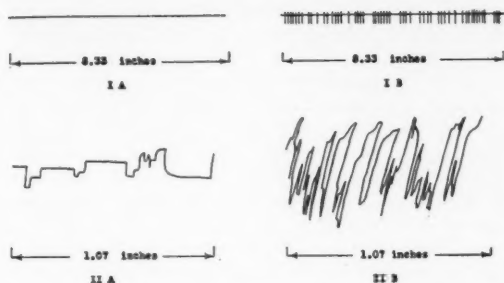
FIG. 14. Sections of activity unit and marking-lever records made simultaneously for comparison of methods regarding tendency to overlap units and to register activity while animal is in its seclusion niche. For values of units in comparison to totals, refer to Table and Figure 5. I, records by activity unit method. II, records by "direct" lever method.

A. Copies of record for 10:00-11:00 A.M.

B. Copies of record for 5:00-6:00 P.M.

For the recordings shown in IA and IIA, the crayfish did not leave its seclusion niche (checked by direct observation for the entire period). Compare the amount of error occurring in IIA with the significant result of IA. For the "direct" lever method (IIB) at a time when the animal is intensely active (5:00-6:00 P.M.), the percentage of activity occurring (in proportion to the total for the 24-hour period) is underrated, and is shown in its true proportion of occurrence by the unit method (IB). (This is an error of 47%. $17 - 9 = 8$; $17 \div 8 = 2.125$; $100 \div 2.12 = 47$). This error is due in part to overlapping of units and is illustrated graphically in Figure 5 for the period from 5:00-6:00 P.M.

The principle outlined has been realized by physiologists since Ludwig and his associates employed the kymograph in physiological experiments. It is presented here only because its importance has been overlooked in many animal behavior studies. Stated briefly, the principle is that a kymograph record is false as long as an increased rate of supplying recording paper would change relative values of record marks; while, of course, rate of supplying paper is constant for each experiment (Fig. 11).

ERRORS BROUGHT ABOUT BY DIRECT METHODS, ESPECIALLY WHEN EMPLOYED IN CONNECTION WITH A 24-HOUR KYMOGRAPH DRUM

1. Activity record marks usually represent unequal values.

In order to better understand values of vertical or slanting recording lever marks of different lengths, one may investigate rates of locomotion of the animal being studied, perhaps only to find that as for a crayfish, average rate of locomotion is ordinarily practically the same whenever it takes place at a definite temperature. Apparent difference in rate is often in proportion to the extent locomotion is interrupted by rest periods for the crayfish, *Cambarus virilis* Hagen (Fig. 13). However, this is beside the point. It is important whether marks would be equivalent in value providing rate of locomotion is constant. If rate is constant, differences in length of vertical or slanting marks are not of qualitative
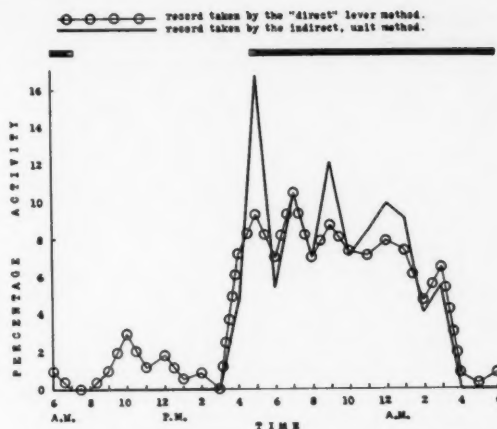
FIG. 15. Activity curves of *Cambarus virilis* Hagen, one based upon a record produced by the activity unit method used in connection with a chronograph that provided eight inches of recording paper per hour, the other based upon a record made by means of the lever method used in connection with a kymograph that provided one and one-fourth inches of paper per hour. Both records were produced simultaneously by the same individual. The direct method indicates that only 90 per cent of all activity is nocturnal, while the indirect (electrical) method shows that practically 100 per cent of activity occurs at night. The hour in which darkness falls and the hours of darkness are considered nocturnal. Assume that the direct method indicates an animal's activity to be 80 per cent nocturnal. This should mean that the amount of activity which occurs at night is four times greater than that which occurs during the day (80/20; 4/1). Assume that the activity unit method in connection with the relatively rapid chronograph indicates activity of the same animal to be 90 per cent nocturnal. This would mean that the nocturnal activity is nine times greater than that which occurs during the day (90/10; 9/1). 90 per cent would be practically correct, and the extent of error can be determined by comparing the incorrect ratio of activity to the correct ratio. The approximate error obtained through the direct method is 55 per cent ($9 - 4 = 5$; $9 \div 5 = 1.8$; $100 \div 1.8 = 55.5$). Based upon Table 2.

significance, that is, do not indicate rate of action but are quantitative in proportion to amount of locomotion and duration of time in which such locomotion occurred. The greater the vertical or horizontal space covered by vertical or slanting activity marks, the greater the duration of activity that is represented (Fig. 12).

Rate of locomotion is indicated only by degree of slant of activity marks; the nearer the mark is to being vertical, the more rapid the motion; the slower the movement of an animal, the nearer will the activity mark be on the horizontal plane that represents inactivity. This criterion is the only one that indicates rate of motion.

The error in evaluating activity marks which are not equivalent in length is reduced by use of a relatively rapid chronograph, especially when the sum of activity periods—as measured by proportion of kymograph record space covered by slanting lines—is compared to the sum of rest periods—as meas-

ured according to proportion of space covered by horizontal lines—and the comparison evaluated as a ratio or per cent. Illustration: if the total horizontal space covered by horizontal lines per 1.07 inches per hour amounts to 0.535 inches and the horizontal space covered by slanting lines totals 0.535 inches, the activity for this hour represents 50 per cent of the amount of activity which would be possible for any hour and would be tabulated as 50. To make such determinations requires careful measurements. The task is time consuming and for this reason is probably not practical, although far more accurate than is the method of attempting to translate directly recorded activity marks into activity "units." It is concluded that for direct recordings, vertical or slanting activity marks are generally not equivalent to each other, regardless of the rate at which the kymograph paper is provided (Fig. 12).

The questions are sometimes asked: (1) "Is it necessary and desirable to determine activity curves to a high degree of accuracy, since they generally vary for each individual from day to day and among individuals of the same species?" (2) "Is it necessary or preferable to analyze for comparison activity periods of less duration than an hour?" "Do not comparisons of hours of activity to hours of inactivity satisfy requirements of significant knowledge?" These questions can be answered as follows: (1) It is not so important to determine activity curves to exact accuracy as to admit in every research the amount of error permitted by methods of measuring activity when and where considerable degree of error occurs. It is necessary to be reasonably accurate in order that the results be in the least significant. To illustrate: if an activity curve shows 60 per cent nocturnality, and the amount of error offered by method of measurement amounts to 18 per cent, it is within a reasonable possibility of error that the activity is actually arhythmic or predominantly diurnal. (2) For the purpose of accuracy in deriving nychthemeral activity curves, it is necessary to analyze an animal's activity within every hour and finally to every minute and fraction of every minute of day and night. This would not be necessary if the activity of animals occurred entirely within one period, that is, either day or night (so far as determination of percentage nocturnal activity is concerned), and it is not necessary for determining whether animals are to some extent active during day or night, or during the various hours. However, if one's interest were confined to what hours species are active and

inactive, such information could best be shown by a check system, the hours in which activity occurs merely being checked so as to contrast them with hours in which activity does not occur. It is necessary to determine the percentage of an animal's activity that occurs during each hour of day and night in detail so far as is possible in order to determine the relative distribution of activity and quiescence through day and night. Accurate results can be secured only by determining the proportion of total duration of activity as compared to total duration of rest periods for night in contrast to the proportions of activity and rest during the day.

The proportion of activity which occurs during the night may be compared to the total as percentage nocturnal activity. The importance of such percentages has been well explained (Park 1937, 1940, 1941, and other references listed in his bibliographies). This type of result is significant from ecological as well as physiological standpoints as illustrated by the following example. If an animal were active on the average one second out of every fifteen during the day, and ten seconds out of every fifteen during the night, it would be ten times more active at night than during the day. This difference probably has ecological significance. It indicates that the animal's community influence and contact should be correspondingly greater at night. It infers that a correspondingly greater amount of area is covered by the animal at night, accompanied by a greater amount of food encountered and an increase in number of enemies attracted as a result of the animal's motion. It should be emphasized that although ecologists are interested in knowing such differences in proportion of activity (as illustrated above), such differences in distribution of activity are not revealed on the 24-hour kymograph drum when used in connection with direct marking levers or cage movements. This is because all space of the record would be completely filled with activity marks and the record would appear to represent arhythmic activity. The errors in this instance amount to zero for the diurnal part of the record, and nine tenths of the correct value (90 per cent) for the nocturnal part of the record.

2. Seclusion niche activity is not distinguishable from community activity.

Activity in seclusion niches registers as equivalent to community activity when activity is recorded by means of levers attached directly to animals or when activity is recorded only by suspended cage movements.

TABLE 2. Activity records taken simultaneously according to two methods. ♀ 38, Dec. 20, 1940.

	TIME–A.M.						TIME–P.M.											TIME–A.M						Total (100%)
	6–7	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	
Activity— Unit Method..	Activity units:										15	53	17	33	22	39	23	27	32	30	13	18	0	0	322
	0	0	0	0	0	0	0	0	0	0															
Recording— Lever Method..	6	0	0	6	16	7	11	3	5	1	43	56	42	62	42	53	44	43	48	44	28	39	5	2	606

Activity that is recorded while an animal is in its seclusion niche cannot be distinguished from locomotor or community activity when methods as described above are used. The occurrence of this error is illustrated for the crayfish, *Cambarus virilis* Hagen in Figures 4 and 5. Such an error would not tend to occur for animals that are generally sedentary, for example, ant-lion larvae; nor for animals that do not remain in limited, secluded areas during periods of comparative rest; nor for those animals that remain motionless during their periods of least activity. This problem has been solved through different means for various animals (references noted below in connection with technical difficulties). For crayfish, activity unit switches have been used to regulate magnetic recorders. Activity units are registered on chronograph paper that moves sufficiently rapidly to prevent overlapping of marks (Roberts 1940, 1941). Activity of an animal while in its seclusion niche may or may not be registered according to the way the apparatus is adjusted to possible positions that animal may take. For experiments upon which Figures 4 and 5 are based, apparatus was so adjusted that activity was not registered for animals while they were in seclusion niches. It is considered that a correct distribution of community activity is shown by activity-unit methods. Observe the general amount of error according to individual hours (on the average) as shown graphically in Fig. 15. The exaggeration of activity during the day in the direct method is due to recording of activity while the animal is in its niche; underrated activity at night in the direct method is the result of overlapping of units, since overlapped units do not show for counting. Refer to Figs. 14 and 15.

<center>UNNATURALNESS OF ENVIRONMENT AS A POSSIBLE
CAUSE OF DISCREPANCY</center>

When studying animals, it is important that they be exposed to the total complex of environmental influences to which they are normally subjected in their natural environments. This point has been explained by Shelford (1934).

It is widely recognized that but few animals on a psychological level as high as that of birds are likely to regulate their feeding and other activities normally when transferred from their natural environment to ordinary laboratory conditions. Such animals must usually be subjected to laboratory conditions for a long period or be reared in captivity, sometimes for more than one generation, before activities are likely to be regulated to occur at normal times.

Activity records of toads have been made in this laboratory, direct observation and unit apparatus being the usual methods employed for recording. Toads were connected to counterweights by way of nylon thread tied at the knee region. During the process of automatically recording activity of amphibians, it has been possible to provide animals with large aquaria, three feet in length placed so as to tilt towards one end. The lower half serves as a pond area, the upper half is a soil and grass terrarium. Activity records resulting through use of unit apparatus in connection with an environment offering a variety of conditions do not show the extremes in degree of activity as appears when animals are confined to very small (directly recording) activity cages. This holds true for toads whether a small tray of water is or is not included in their container. An explanation may be that toads tend to go to water and remain in water to some extent at night during the breeding season. If a suitable body of water that can be easily recognized by toads is not available, their activity becomes exaggerated in degree above that which would be normal. A problem that is not yet completely solved in this connection is how toads find water. Toads have often been observed to climb a foot-high fence situated across one end of a backyard and continue their course to a lily pool that is thirty feet from the fence and not visible from ground-level at that distance (Knipp 1941).

Unit apparatus of the electrical type will probably not prove useful in activity studies of small mammals, since individuals of some species at least spend considerable time biting or clawing any harness into which they are placed. This is true for the mouse, *Microtus ochregaster* Wagner (experiments not published). Methods of obtaining separate records of niche and community activities of vertebrates, etc., are presented in connection with technical difficulties.

<center>SOLVING TECHNICAL DIFFICULTIES</center>

The problem of separating seclusion niche and community activity is solved for the house wren, catbird, robin, and phoebe with especial regard to parental care and community activity by having an electric treadle switch situated at nest entrances. For this method, different positions taken by a double magnetic reorder (operated through two treadles in a single pathway) indicate the time at which animals leave or enter their niches (Kendeigh & Baldwin 1930). By having separate exit and entrance tunnels connected with a nest box, an electric treadle switch in each pathway and a one-day door at each end of both tunnels, magnetic recorders indicate when an animal enters and leaves its nest (L. Foss 1941, personal communication). For the wood rat, a pendulum switch is situated at the entrance of a niche (Spencer 1939, 1941). A contact is placed on both sides of the pendulum, each one leading to a double-magnet recorder as for the Kendeigh-Baldwin method. The time at which an animal is in and out of its niche is indicated by the position of the line that is drawn by a magnetic pen on a chronograph tape.

The space within which an experimental animal can move is quite limited when it is attached directly to recording levers. A recording lever can be balanced carefully by a light counterweight when mounted on jeweled pivots. If glazed smoked paper on a Harvard kymograph is used in connection with such a lever, friction and the limitation of space

available to an animal are at a minimum for direct levers. Similar levers have been used in physiological research for a considerable period.

For pulley and sliding-bridge activity unit switches, space that the animal can cover is not limited beyond a reasonable degree (that is, not beyond that which it is practical to provide for laboratory or field experiments), since a pulley switch may be placed sufficiently high to allow a leeway of a number of feet for the counterweight (Roberts 1941, 1941a, 1941b). Also, the length of sliding-bridge switches may amount to several feet. In the several types of apparatus which do not require direct connections between animals and apparatus, space available to animals is not unreasonably limited, if limited at all.

The possibility that a direct connection to an animal may alter activity has been stated (Spoor 1941). This is reasonable for instances in which a pull upon experimental animals is more than negligible, and probably holds for all organisms having nervous systems sufficiently highly developed to enable them to be aware of being attached. Unit switches require such light counterweights (as low as .02 gram) that the pull upon ordinary animals is insignificant; that is, more than counter-balanced by the animal's own weight. All but the smallest organisms can move about in any direction without showing any exertion. During two years experience in using unit apparatus in connection with certain crustaceans and amphibians, animals have never shown evidence that their attention may be focused upon, diverted by, or influenced by the thread that connects animals to counterweights.

A very valuable contribution is offered for measuring fish activity by a method that does not limit the space an experimental animal would normally tend to take (Spoor 1941). The same method does not require a direct connection between animal and apparatus, and as stated by Spoor omits the existence of a factor that may in many instances be an adverse influence and source of error in measurement of activity. Through using a number of apparatus units each one leading to a separate recorder (and probably also by adjusting sensitivity), this apparatus provides a means of measuring locomotion as distinct from mere fin movement.

There are several methods which do not require direct connections between animal and recording apparatus. These include: treadle methods (Kendeigh & Baldwin 1930; Fautin 1941; Foss 1941; R. Lindeborg 1941, personal communication); other treadle methods (Lutz 1932a, 1932b; cf., Park 1935; Park 1935); the pendulum method (Spencer 1939, 1941); audio-frequency apparatus (Emerson 1929; Park 1937); a drop-bar activity apparatus (Wright 1939); the piezo-electric recording apparatus (Odum 1941; Odum & Kendeigh 1940); the paddle-switch method (Spoor 1941); and tambour-controlled activity apparatus (Szymanski 1914). Observance of tracks at hourly intervals has also been employed as a means of determining the times at which certain animals are active (Szymanski 1918). By using several strategically spaced apparatus-units it should prove possible to measure locomotion as distinct from other activities by several methods including the following: the audio-frequency method, the piezo-electric method, treadle methods, and tambour-controlled recorders. Some of these modifications and other methods are probably in use at present. Ordinarily, methods are limited in some respect either in being practical only for aquatic animals or only for terrestrial animals, or they may be capable of measuring activity of only relatively large animals.

SOME FACTORS THAT MAY ACCOUNT FOR VARIATIONS IN RESEARCH RESULTS

1. Reaction to light may be reversed or prevented when animals are subjected to temperatures above or below certain levels. This phenomenon occurs for certain copepods (Loeb 1893), certain crayfish (Bell 1906), and leaf-mining beetles (Chapman 1923).

2. Reaction to light may be reversed or checked by chemical influences. The aquatic mites, Unionicola, are positive to light when in pure water. When stimulated by dilute chemicals that emanate from clam tissues, these mites are negatively phototropic, possibly as a result of conditioning of photic response to light during immature stages (Welsh 1930). Also see Loeb 1900, p. 198; Barnes 1937, p. 339.

3. Evidently phototaxis may change with height of tide, becoming negative when the tide is high and positive when the tide is low. This behavior is illustrated by Littorina as observed by Bohn (cf., Holmes 1911, p. 157). See point 13.

4. Reaction to light may change according to whether illumination is direct or diffuse, as illustrated by *Cambarus affinis* (Bell 1906).

5. Reaction to light may change from positive to negative in accordance with intensity of light. Manner of reactions to various influences (light, pH, etc.) depends upon intensity of the stimulus (Warden *et al.* 1940).

6. Reaction to light and shade of background may vary for crustacea according to the proportion of light that reaches the dorsal, lateral, and ventral surfaces of the eyes, as illustrated by certain shrimp and crayfish. How these animals react to light depends largely upon whether the background upon which they rest is light or dark (Keeble 1904; Brown 1934).

7. Change in light intensity may regulate the manner in which adult toads react to air and water (see text).

8. A minute "pin-hole" trace of light may bring about maximum response, as illustrated by influence of light on chromatophores of Macromysis (Keeble 1904). It is important therefore either to keep "darkrooms" perfectly dark or to provide constant illumination when investigating whether endogenous rhythms synchronize with day and night.

9. Reactions of animals to light may require such a long time that investigators might conclude light exerts no influence. When Hippolyte is transferred to an environment characterized by background colors different to those to which it has been accustomed, about seven days are required before color adjustment to new surroundings takes place (Gamble & Keeble 1900; Clark 1921; cf., Pearse 1939).

10. Immature animals may respond one way to light and adults in a different way. This phenomenon has been observed for the shrimp Palaemon (Keeble 1904) and crayfish, *Cambarus affinis* (Andrews 1907).

11. Males may react differently to light than do the females of the same species. This type of behavior difference between sexes has been described for certain copepods (Parker 1902; cf., Pearse 1939).

12. Feeding may reverse or check reaction of animals to gravity. This is noted to occur for certain caterpillars (Loeb 1918).

13. Changes in barometric and water pressure may reverse or check response of animals to gravity. This influence of pressure upon reaction to gravity has been described for *Cambarus affinis* (Bell 1906).

14. Touch may check photo-response in the shrimp Macromysis (Keeble 1904).

15. Temperature differences may alter the manner in which animals respond to gravity. This phenomenon is illustrated by *Cambarus affinis* (Bell 1906).

16. Significant results cannot be obtained if animals are allowed to become fatigued unless a special problem of studying fatigue is undertaken. Behavior of crayfish illustrates this point (Kalmus 1938; Roberts 1941a).

17. Quantitative variations in an environmental factor may bring about qualitative differences in biotic phenomena as shown by recognition of colors.

18. Behavior differences may result from influence of environment on structure. In turn, modified behavior may assist in bringing about further modification of structure. See modified growth phenomena.

19. Responses to stimuli may be reversed as a result of internal changes that occur without relation to external influence, such as changes brought about by reaching sexual maturity (Shelford 1937, p. 30).

20. The inherent nature of particular individuals that are selected for study may account for apparent discrepancies of research results (Crozier & Hoagland 1934).

21. The kind of stimuli to which animals are exposed and the extent that animals are conditioned to stimuli just previous to their subjection to change in intensity of stimuli are factors of importance in modifying behavior.

22. Past conditioning through the formation of nervous associations or conditioned response tendency may influence experimental results. Consider the nature of Unionicola's response to light.

23. It is not safe to make physiological tests on organisms nor to take extracts from organisms for experimental tests only during the day since endogenous rhythmic influences may modify physiological states and behavior tendencies. Endogenous influences may be sufficiently powerful to dominate or camouflage effects of stimuli to which animals are subjected for experimental tests.

24. Averages of many records do not reveal endogenous rhythms except when such rhythms synchronize with definite influences. Therefore, there are instances when single activity records reveal more than averages of many records.

25. The percentage of activity which is nocturnal and diurnal for exogenous nychthemeral rhythms has often been based upon the proportion of activity that occurs from 6 P.M. to 6 A.M. as compared to the amount of activity that occurs in the 24-hour period (6 P.M. to 6 P.M.). This permits a great error when night and day are quite different in length. Also, night may not begin at 6 P.M. It is proper to determine percentages of activity that occur during periods of special environmental factor complexes by comparing the amount of activity that occurs during hours of darkness to the amount of activity that occurs during day-light hours.

26. For averages of environmentally controlled rhythms, such as light-controlled rhythms, activity records of the first hours that immediately follow daylight should be averaged together and activity records that immediately follow darkness should be averaged together.

Hours that immediately follow daybreak and those that immediately follow darkness should be spaced twelve hours apart. Averages for the hours of activity for the intermediate hours should be spaced for averaging in reference to times that darkness and daylight begin and not in regard to clock time. When periods of thirteen hours or more are reduced to twelve hours as when days or nights are longer than twelve hours, those hours that overlap may be dropped or averaged. When days or nights are shorter than twelve hours, the spacing of daybreak and dusk to twelve hours apart leaves a gap of one or more hours. This gap may be filled by intercalation. The averages of activity for the hours on each side of the gap may be merely connected by drawing a line between two points plotted on a graph of activity.

This system is the only one that permits a standardization of activity curves. If this method is not followed in averaging environmentally controlled rhythms, the averages of activity peaks tends to flatten due to the fact that night begins at a different time each day.

SUMMARY AND CONCLUSIONS

1. When recording activity on a 24-hour kymograph drum, there is great possibility of error as a result of overlapping of units for direct activity-lever attachments and suspended cage movements.

2. Activity marks made by levers attached directly to animals or to cages do not represent equivalent amounts of activity, and do not merit numerical translation into units, unless one cares to measure

the relative lengths of the activity marks in order to determine their values. The latter procedure is so time consuming as to hinder progress.

3. For any given period—for the same methods as mentioned above—duration of activity can be determined by comparing amount of horizontal kymograph space covered by horizontal lines to the amount of horizontal space covered by slanting lines, but this method is also too time wasting to be desirable.

4. When these direct methods of recording are employed, activity of an animal while in its seclusion niche registers as general activity, and community activities are not distinguishable from seclusion niche activities.

5. Activitiy curves based upon general body movement have only physiological significance. The times at which particular kinds of activities occur is of ecological significance.

6. Population densities based upon the number of active individuals in time communities are more likely to be ecologically significant than population densities based upon the total numbers of individuals in place communities. Diurnal and nocturnal communities possess their own population densities.

7. Environmental conditions to which animals are subjected for activity recordings and laboratory observations should resemble conditions of an animal's natural environment as closely as possible. All environmental influences should be allowed to fluctuate at a given time in a reasonable portion of experiments. Generally, a portion of experiments requires constant conditions, and another portion requires that all influences remain constant except one. Laboratory studies of behavior should be supported by field studies.

8. Knowledge of activity of immature animals is as important as that concerning adults.

9. It is as important to know the nature of activity of animals out of the breeding season as well as that which occurs during the breeding season. It is important that activity researches state whether animals are studied in the breeding season.

10. Probable trends in the evolution of several behavior traits are given. Their consideration elucidates relationships between different characteristics and assists in augmenting the significance of a classification.

Complex behavior traits are reached via evolutionary processes through stages of less complexity. After a stage of complexity is once attained, evolution may follow a course towards greater complexity or greater simplicity. This is an illustration of organisms taking lines of least resistance so far as particular inherited and environmental equipment are involved. That which represents maximum simplicity for one kind of organism may be the most complex route possible to another type of organism.

11. A force or phenomenon may manifest itself (with our limited ability in detecting biological phenomena) only in what would appear to be exceptions to a rule. To emphasize the importance of this fact can assist in discovering obscure physiological

rhythms and in finding the existence of behavior tendencies that appear to be absent in the majority of examples. By following this idea instead of concluding that definite landmarks are important for the orientation of all birds, it was possible for a branch of the United States army to develop night-flying homing pigeons. Consider also: the average interval in occurrence of pronounced locomotor activity for a crayfish when kept in constant darkness. The average interval (about 24 hours) and its significance are not apparent without application of mathematics to data.

12. Biological science should advance more efficiently and at a more rapid rate when it is assumed that entirely new—and perhaps unthought of—mechanisms may exist to control commonly observed phenomena, rather than assume that mechanisms probably already known through studies of some organisms should account for phenomena thus far unexplained in other organisms. Conclusions concerning the importance of landmarks for the homing of some organisms have been given prematurely, and chance has sometimes been offered as a possible explanation without support of computation of mathematical probability. An important attitude in research has achieved results in a study of orientation in bats, and may lead to valuable discoveries in connection with mechanisms that enable both bats and homing pigeons to return to home areas over extensive unknown territory.

13. The fact that many animals are brilliantly colored is not evidence that protective coloration is of little value. Brightly colored animals have some other adaptation that replaces and is equivalent to adaptation of resemblance to surroundings. Also, bright color is useful in many instances.

14. A synopsis of behavior of organisms is presented. Activities are subdivided so that different adaptations that meet the same ends may be compared so as to illustrate parallelism, adaptive radiation, and convergence of behavior adaptations.

15. Mere growth or secretion for some organisms is perfectly comparable with and equivalent to dynamic activity of other organisms. Nutritive, reproductive, and protective activities, trap mechanisms, repulsion mechanisms, means of anchorage, means of dispersal, and methods of shelter securement are represented by passive activities in some organisms and by their equivalents in dynamic activities for other organisms. Therefore, passive physiological processes belong to the field of behavior in many instances.

GLOSSARY

Adaptations and adjustment:

The meanings of adaptation and adjustment are often confused. Any structural, physiological, behavioristic, or psychological traits that help an organism, or aggregation of organisms, or a species, to survive is an adaptation. *Individual adaptation.* Adaptations of individuals consist of equipment and abilities that meet life requirements while learning

from other individuals is not involved. Equipment and abilities already referred to may involve tendencies or motives. The environment to which adaptations are suited may be static or changing. The abilities to carry out adjustments are always adaptations, but not all adjustments depend exclusively upon adaptations. This applies in those instances in which adjustments depend upon acquirement of methods, tendencies, or motives through training or encouragement received from other individuals. *Adjustments* are always processes of improvement in the adaptiveness of self in the meeting of life requirements in response to changing environmental conditions. Some adjustments may be made by reliance upon nothing but inherited equipment. Such adjustments are equivalent to adaptations. On the other hand, some adjustments depend upon acquirement from other individuals of tendencies, motives, or learning of methods that play a part in adjustment. In such instances, more factors than possession of adaptive abilities are involved. An example of such an adjustment is the recovery from certain mental ills where outside aid is required (Sci. Dig. 1942). *Species adaptation.* A species adaptation involves whatever is necessary to carry out a useful act. For primitive man securement of food involved teaching new individuals how to hunt or grow crops plus the ability to learn and carry out the methods learned. Many adaptations and adjustments are described by Pearse (1939).

Autecology:

Autecology deals with relations of individuals to their environments. It often makes use of physiological experiments to obtain knowledge and so tests the responses of parts of living organisms (Pearse 1939, p. 1).

Community activity:

Community activities of individuals and groups of animals and species are those activities that involve or are likely to influence other individuals—including at least those of different species. Since animals are likely to influence other species such as predators by exposing themselves through movement in the open, "exposed activity" is equivalent to community activity. Locomotor activity is an important community activity. Locomotion correlates so closely with exposed activity that it may be used to measure community activity. It is convenient to refer to locomotion as a synonym for community activity when it is understood that locomotion occurs in the open and represents exposed activity. These terms apply to those animals that move about to get food and are especially useful in application to animals which take to shelters during periods of quiescence. Strictly speaking, community activities include: securement of food, retreat or attempts to escape from enemies, movements that attract predators to them or result in their being caught by a predator; for instance, locomotion of ants that results in their falling into the traps of ant-lions. Community activities are based upon interspecific relations (Pearse 1939, p. 498-533).

Compound instinct:

In compound instincts, completion of one act serves as a stimulus or release of a new tendency for starting another type of specific action. Successive activities depend upon a chain of stimuli, most links of which are generally brought about by an animal's own activity.

Consciousness, desire, and volition:

Consciousness is a reality only to the extent that it is an abstract function of complex nervous systems, experiences of which nearly coincide with actuality. In consciousness, specialized protoplasmic mechanisms act as intermediaries between conscious centers and environment. In subconsciousness, the conscious center is isolated from environmental stimulation so that mental experiences depend upon inherited mental equipment and past stimulations received and experienced in relation to actualities. Consciousness is a product of perceptions received through all of the senses available to an organism, and may be in part a result of an assumption, sensation, or belief that objects and experiences are actual. The subconscious state may be fooled in dreams. A nerve center may experience sensations of being conscious as a result of recurrence of impressions while no synchronization exists between mental experience and actuality. This type of mental experience falls short of being consciousness only because mental experience is not directly related to actual happenings, and is not as vivid as normally results when experiences and perceptions are created through direct environmental influence. In consciousness, each sense enables its own contribution to be created as a space concept within a special nerve center. Each contribution is a part of consciousness. All that appears to an organism as occurring in its environment is known only through what occurs in an animal's own nervous system, for all objects and movements that seem to occur in the environment are imagined to be in space by a phenomenon of the imagination which is the most important aspect of consciousness. Visual and all other perceptions to include physiological pains are not sensed where they seem to be located. A pain in an arm is not actually felt in the arm. This fact is illustrated by the occurrence of sensations that seem to be located where injured limbs once existed previous to their amputation. Pains are real but their apparent locations are projected entirely in the mind. Sounds are not heard at a distance but within protoplasm. It is equally true that a cloud is not seen in the sky but in the mind by being projected into mental space. This point becomes clear when it is realized that visual perception of depth arises from stimulations sent to conscious centers from almost flat retinal surfaces. Consciousness is a specially modified "subconsciousness." Consciousness is equivalent to a dream (a phenomenon of the subconscious), experi-

ences of which are made consistent, vivid, and guided to a great extent through sense perception. This is so literally true that these qualifications of subconsciousness serve to define consciousness. Conscious mental experiences do not necessarily represent a true nature of objects perceived, nor do conscious perceptions take place at exactly the same time as perceived phenomena occur.

The archer fish, mantis, chameleon, and kingbird experience perception through consciousness. This logical conclusion relies upon the following considerations. The animals mentioned prove by their actions that they perceive depth in visual experience. Through mental experience, these animals recognize the distances visual objects and sources of sound are away from their own positions. This fact is demonstrated by the high degree of accuracy these animals employ in striking and catching their prey. They do not reach or grab for their food until it has been approached to a distance that is appropriate for successful contact. The archer fish can hit flies by squirting water to distances of several feet. A chameleon is capable of striking flies with its tongue without error at distances of several inches. Nasuate termite soldiers are capable of squirting juice upon enemies within fairly close range without employment of visual perception. (It may be that termite soldiers sense positions of enemies. However, no attempt will be made at this time to apply this reasoning to termites.) Both locomotion and trap mechanisms are guided accurately in relation to position of prey.

These considerations provide logical proof that such animals as fishes, mantids, chameleons, and kingbirds project what is perceived into space through consciousness, that is, via a phenomenon of imagination. Their perceptions are projected into space as mental abstractions that represent realities. It has been mentioned above that such perceptions as mental space conceptions are a part of an animal's consciousness; in fact, that mental space-creation is consciousness when practically coincidental with actuality due to environmental stimulation.

Desire is a nervous phenomenon that can be experienced by either "consciousness" or "subconsciousness" in relation to concepts of objects or experiences that symbolize mental satisfaction or pain. Objects or experiences may become symbols of satisfaction or pain through experience (conditioned mental experience), or through imagination (trial and error or random thinking), especially when in combination with wishful thinking. Desires and wishes do not depend directly upon consciousness, for they can be experienced in subconscious nervous states (dreams).

It is reasonable that desire and volition are qualities of conscious mental experience when behavior is modifiable according to nature of past experience and consciously controlled. This reasoning is applicable to many lower animals as well as to man and is based upon the only available explanation for behavior that is both modifiable and consistent in accordance

with peculiarities of objects and acts that are abstractly perceived when peculiarities of objects and actions are responsible for the nature of symbols formed which are in turn responsible for repetition or inhibition of acts. This explanation is as follows: some acts and objects become symbols of "satisfaction" through past experience. It is recognized that the most primitive type of satisfaction may be represented by absence of pain. Some acts and objects become symbols of pain. Some activities are controlled through stimulation by objects and happenings that symbolize neither pain nor satisfaction according to observed reactions. Such activities may be carried out through self-guidance, and organisms may or may not be conscious of these activities. Such activities never can serve as evidence that desire, volition, or consciousness accompany activities.

Symbols are perceived through mental abstractions, that is, as conscious conceptions. Definite positive or negative conscious reactions to symbols are based upon mental tendencies. Tendencies—so characterized—are known as desires. Employment of this criterion to judge when desires occur in animals reveals that many other animals besides humans are capable of experiencing desires. This is not an indication that any lower organisms are ever capable of realizing consciousness of their desires. Consciousness of one's own desires involves "self-consciousness" which is practically lacking in all animals except humans and probably certain apes.

Confliction of desires or confusion results when an object becomes a symbol of both pain and satisfaction, or when two or more like symbols excite an animal simultaneously.

When desire is responsible for instigation or execution of action, such action is designated as voluntary. Thus, organisms which are capable of experiencing desire are also capable of experiencing volition. This does not mean that any lower organisms are conscious of a sensation of volition experience.

Volition is performance of an act guided by desire. Voluntary actions are those dependent upon desire for their instigation or/and execution. This definition of volition also serves to define "free will." Desire may or may not be dependent upon forethought, sense of right and wrong, aesthetic sense, physiological drives, learning, training, or emotions. Desire may or may not amount to an emotion in some human activities carried out by volition. Desire may be dependent upon a determination to illustrate that any desire can be inhibited or carried out at a time chosen by a performer. In the latter instance, a line of least resistance is being followed as for all others; since an original desire is dominated by a new and greater desire. In this instance a desire to inhibit or carry out an action is dominated by a desire to demonstrate "free will." A principal desire can initiate the subdesires necessary to carry out a main objective. Behavior is at the mercy of desires for animals that recognize symbols of pain and symbols of agreeableness.

Origin of desire and volition undoubtedly precedes or arises coincidentally with origin of intelligent action. This is shown by the fact that children realize desire and volition before intelligence becomes functional. It is not strange that desire and volition should occur to some extent in those lower animals which show some intelligence. As previously explained, behavior of animals that is very readily modified when associated with conscious perception of pain is an instance of intelligent action. The converse tends to hold true. Humans that do not possess the ability to learn to inhibit acts when punished show lack of intelligence and are likely to possess the mental development of imbeciles. However, refusal to learn as a result of powerful endogenous countertendencies does not prove lack of intelligence. Animals that are capable of learning readily through conscious reactions include some fishes and animals above the fish level of complexity that reveal evidences of consciousness.

A question as to whether desire, volition, or consciousness exist in many lower organisms should not remain after these points are considered. Logic and the rule of parsimony require that the probabilities mentioned should be assumed unless negative evidence can be provided. At present the only sensible question that remains is to what extent vividness of volition, desire, and consciousness occur in different species. In some organisms, existence of these qualities must be zero. There should be intergradations in vividness of sensation from zero in the lowest organisms to a state of extreme realization in human beings.

It is now realized that desires are not dependent upon nervous systems alone. They are in some instances at least indirectly dependent upon hormonal influences which modify nervous centers. This has been demonstrated by glandular studies of peck order and parental care in fowls. With proper hormonal influence, a weak hen will become dominant over other hens of a flock; and a young pullet will become a foster parent. That some desires are similarly controlled in humans has also been proved by sex injuries, operations, and reversals. Chemicals may evidently bring about their influence upon instinct by modifying central nervous centers or through effect upon effectors.

It is within the realm of logic to show that consciousness, desire, and volition are phenomena experienced by some lower organisms. Although it is beyond human comprehension at present to understand how protoplasm or matter of any sort can acquire abstract properties of consciousness and emotions, there is reasonable proof that the nature of consciousness and desires has a mechanistic basis as evidenced by studies of mentality and character of identical twins, geniuses, and the intellectually incompetent, and as evidenced by comparisons of desires and behavior tendencies of persons before and after brain operations (reference: authorities in the fields of psychology and medicine and Sci. News Letter).

Anthropomorphic interpretations are formed by what is implied by similarity of behavior of lower animals to the actions of and associated sensations of man. Anthropomorphic interpretations are unscientific and are naturally to be looked down upon.

Conclusions drawn by way of logic are not anthropomorphic. It is not what is concluded but the manner in which conclusions are drawn that counts.

Summary: Mental images have usually been considered to belong to one of two classes: (1) concrete images when created through sense perception, (2) abstract images when occurring in mind as after impressions (memory) or imagination (modified after impressions and mental creations). This differentiation does not have a sound basis. All images that are experienced in mind are abstractions. The only differences between images that are created through sense perceptions and those that occur as after-impressions are that those images that depend directly upon sense perception for their formation are normally more vivid and more exact than are memories or invented images. Both types of images are created as abstractions in the SAME protoplasm. This idea is proved by the following fact. Motion pictures do not flicker as a result of the existence of after-impressions. This is possible because after-impressions are vivid and exact for a brief period.

An animal that experiences both consciousness (as shown by criteria that reveal the occurrence of mental space creation) and will (as evidenced by criteria that reveal modification of behavior in accordance with the peculiarities of abstract symbols), possesses to some extent those nervous qualities designated as desire and volition ("free will"). In order that this judgment be justified, it must be applied only to initial acts and not to habitual acts, for there must be evidence that guidance of behavior occurs via consciousness and not through mere subconsciousness. (Habitual and unmodifiable acts cannot serve as evidence of will because they can occur via primitive physiological processes.) These principles for analysis of consciousness, desire, and volition should usually be applied without disregard of Morgan's law (cf., Holmes 1911). Scientists are more interested in probabilities than proofs. Most research data are significant according to coefficients of probabilities and are not proofs in a literal sense. The criteria offered to determine whether mental phenomena of animals are on the psychological level can never give positive proof of consciousness. However, what is expected for proof can be carried to a point of absurdity.

It is unreasonable to regard simple animals such as protozoa and others which do not have specialized senses and a brain as capable of experiencing consciousness to any extent, because we cannot conceive of the existence of a phenomenon unless some criterion or evidence or logic can be produced for the formulation of belief. This problem cannot be answered for those animals in which it cannot be determined whether mental space-projection phenomena occur. In cephalopods, higher crustacea and

insects, and all but the simplest chordates there is evidence of consciousness, and many experiments that have been carried out to determine the nature of modifiability of behavior reveal evidences of desire and volition.

According to Webster, desire may be defined as conative consciousness or (conscious) inclination. In this treatise, pain and satisfaction are employed in the broadest sense. Pain can be experienced without emotion. Although satisfaction is usually thought of as an emotion, its most primitive equivalent is lack of pain. It is not safe to assume that invertebrates and lower chordates sense pain as a conscious sensation, but some phenomenon equivalent to pain must take place. It is not assumed that lower animals experience any emotions. Pieron's criterion for the occurrence of a mental phenomenon in lower organisms that is equivalent to emotion may possibly be sound when (but only when) it is revealed that conscious abstractions or symbols determine the nature of action (Warden *et al.* 1940, p. 788-789).

Dynamic community:

A dynamic community consists of all the organisms in a place-community which—at any particular time—are actively exposed in the community. Dynamic community means active time-community (Elton 1935, p. 86).

Ecology:

Ecology is the science concerned with relations of organisms to their environment (Adams 1913; Shelford 1937; Elton 1935; Pearse 1939).

Environmental factor:

An environmental factor is a possible or potential ecological influence and may be considered as synonymous with environmental condition. Light, darkness, heat, vibrations, evaporative tendency of air, physical pressure, are examples of environmental factors and become ecological factors when organisms come into contact with them. They are ecological influences in those instances in which they affect organisms.

Exposed activity:

All activities that occur for animals while they are not concealed (either through taking advantage of shelters or by relying upon protective coloration or/and quiescence) are exposed activities.

Habit and rhythm:

Habits are acquired methods or sequences of actions in the repetition of activities. Almost unlimited variation in time may occur in the performance of each of the activities of a complex act. As long as a definite sequence of different actions is correctly carried out, peculiarities that characterize an entire act as a habit are not being violated. The meaning of "habit" as used in relation to method or sequence of different activities is probably more appropriate than the application of this word to acquired periodicity in alternation of activity and quiescence. It is sufficient to characterize rhythmic tendencies as "rhythmic phenomena" without relating this quality of action to habit. A rhythm is periodic release of energy or response to periodic releases of energy, or may involve both endogenous regulation and response. An acquired rhythm is based upon modification of tendency of energy release and may be merely a result of modification in rate of energy release; whereas, all habits are learned actions; not mere modifications of rates of processes. Rhythms may be acquired by single cells. Blossoms of some cacti, such as Cereus, can open and close in continuous darkness as a result of endogenous influences. Many rhythmic biological phenomena originate independently of environmental influences; for instance, the beating of hearts, movements of appendages of fairy shrimps, and electrical activity of ganglia (Prosser 1934).

Individualistic activity:

Individualistic activities are those which concern only the individual. Examples of "personal" activities are: the process of feeding, cleaning the body, etc.

Instinct:

Instinct signifies behavior that is not learned, nor innovated, nor modified by intelligence. When modified, it should be designated as *modified instinct*. The word instinct is important because it has no synonym. Words are invented in order to eradicate descriptive phrases. Simple instinct consists of a single unlearned, uninvented, and unmodified action in contrast to compound instinct which consists of two or more different acts, one following another in a definite sequence. There are modified simple instincts and modified compound instincts. A single link or all links of a compound instinct may be modified. Unnecessary links may be eliminated to give *abbreviated instinct* to illustrate one type of modification. Instinct appears to depend upon chemical conditions of protoplasm (Hartman 1942). Evidently, chemicals may regulate instinct by influencing brains. It is possible that chemicals may modify effectors (Loeb, cf., Livingston 1903; Barnes 1937, p. 338).

Intelligent or intellectual behavior:

Intelligence is capacity to react beneficially to situations that require originality in action or choice of possible actions. Intelligence involves knowledge or understanding or depends upon previous mental experience, and therefore exists only on a psychological level (Webster).

1. In new situations. Innovative or inventive intelligence; that is, reasoning.

    a. Advanced intelligent action. Trial and error thought procedure followed by action. Behavior is guided by forethought, in turn dependent upon employment of mechanical activities, such as, trial and error thinking, inhibition of thoughts that are least adaptive, and selection of the most fit. Efficient thinking is analogous to choice of shortest routes

and reduction in random movements as occurs in animals well experienced in orientation and in finding their way home when released at great distances from their home areas. In man, forethought is at first substituted for physical activity as an indirect route to solve problems that are solved through direct activity by most lower organisms.

b. Primitive intelligent action (Holmes 1911, p. 164-231). Physiological innovative intelligence. Forethought not involved. Trial and error intelligence. Beneficial behavior guided without forethought. Intelligence without forethought probably occurs in wasps that use tools. Lower organisms tend to try out one procedure or another probably without previously thinking about probable outcomes. If an act tried is successful, opportunities for their recurrence comes again. Tendency to repeat successful acts increases as a result of strengthened nervous associations and opportunity is often extended for the reproduction of offspring that inherit a capacity to repeat the same acts. Both beneficial conscious trial and error acts and acts based upon selection of appropriate actions as determined by forethought represent intelligent action. Intelligent actions of human beings are not distinct from those occurring in some lower organisms except that they are often preceded by and guided by abstract trial and error and selective mental processes. Mental tendencies may be considered as determined. They differ according to the manner in which the mind is trained in the use of thought mechanisms. Trial and error mental tendencies are carried out in a manner similar to less abstract and mechanical nervous activities of some "lower" organisms relatively high on the scale of nervous complexity and are also analogous to the trial and error actions of Paramecium.

2. Intelligent behavior dependent upon learned mental associations related to the behavior situation in question.

a. Selection of objects or acts learned through previous personal experience based upon the nature of past experience. Selection of action or objects is determined according to whether acts or objects are symbolized in mental experience as beneficial, pleasurable, or least painful. This type of intelligence occurs for humans. It does not involve innovation. For meanings of pleasurable and painful, see consciousness.

b. Learned through observation of what happens for other individuals.

c. Learned via abstract communication.

Locomotion:

Animals can locomote while in their seclusion niches. However, space in the seclusion niches of most animal species is very limited. It is, therefore, convenient to consider locomotion as occurring in the open unless otherwise stated.

Locomotion is so closely correlated with securement of food and escape from enemies that measurement of locomotion may be accepted as measurement of community activity or exposed activity.

Niche activity:

"Niche activity" as used in this treatise means "seclusion niche activity"; that is, activity of an animal that occurs while the animal is in its seclusion niche. For example, a crayfish may locomote to a slight extent and perform body-cleaning movements while it is in its seclusion niche. Such activities are "niche activities" so long as they are carried out in the niche. Niche activity is synonymous with "concealed acivity."

Nocturnal eommunity:

A night-community consists of all members of a place-community that are active in the open during the period of darkness. The nocturnal community is one of the time-communities, and only those organisms which take part in community dynamics constitute a part of it (Elton 1935, p. 83).

Nychthemeral:

Nychthemeral refers to a period that consists of a day plus a night. It has no synonym. This word has been used repeatedly by Bohn (1903) and Parker (1919).

Physiological ecology:

The scope of physiological ecology has been given by Shelford (1937, p. 299-308).

Psychological:

Pertains to abstract—though not necessarily conscious—mental phenomena.

Place-community:

A place-community consists of all of the organisms within any particular territory characterized throughout by the presence of particular species (Shelford 1937, p. 3; Clements & Shelford 1939; Elton 1935, p. 86).

Securement of food:

Securement of food involves going after food, and often necessitates catching or trapping it with some skill when food is animate. Securement of food is a community activity and contrasts with feeding after food is obtained. The act of eating is an individualistic activity.

Species activity:

Species activity refers to those behavior relations that occur between members of a species. Species activities include mating and taking care of young. Species activity comprises behavior based upon intraspecific relations (Pearse 1939, p. 458-497).

Synecology:

Synecology is the branch of ecology concerned with interrelations that occur among members of particular communities and the relations that exist between plant-animal societies—considered as a whole—and their environments (Shelford 1937; Pearse 1939; Clements & Shelford 1939).

Time-community:

A time-community consists of all of the animals in a place community that are active in the open during a particular time period characterized by a special complex of environmental conditions. Diurnal and nocturnal communities are examples of time-communities.

Tropism:

Tropism does not apply to a class of complexity of response. Tropism must be applied independently of all the known classes of complexity of actions such as instinct, learned behavior, intelligent modification of behavior and creative behavior. Tropism applies to a manner of response, that is, to whether movement of an animal is towards or away from a stimulus. Tropism covers predictable reactions to particular stimuli. It is correct to regard tropistic tendencies as automatic or mechanical although they are not necessarily instinctive. The opinion that tropisms are necessarily instinctive is a misconception that resulted from the fact that the person who first elaborated upon tropisms believed all behavior to be automatic and mechanical in its last analysis. Loeb believed that human behavior is free only to the extent that desires control behavior. He believed that desires are dependent upon what environmental experience does with inherited tendencies and that all of man's behavior follows lines of least resistance. No one has offered evidence that Loeb was mistaken. On the contrary, the results of brain and gland operations prove his views to be correct. However, most zoölogists who adopted the word tropism as soon as it was made available either did not quite understand or did not accept Loeb's point of view. They took the term tropism and applied it only to behavior which in their own opinions could come under the scope of mechanistic philosophy.

Tropisms are natural tendencies. They may be either instinctive or learned through conditioned experience. When higher organisms inhibit a tropistic tendency, a desire (of a high order) is merely dominating a more primitive tendency. If tropistic tendency is experienced in consciousness, it is to be regarded as a desire of either a high or low order depending upon how abstract is the concept of the stimulus. Concepts are abstract if perceived as images that seem to be projected into space. If an organism goes towards or away from a stimulus as a result of intelligence, the act is a tropism, providing the manner of action is predictable. The criterion of predictableness indicates that the nature of an act is within the scope of automatic and mechanical behavior. All behavior would be predictable if all

could be known concerning the heredity of particular individuals, and if all could be known regarding past experiences and their influences.

An illustration of a tropism as it can be experienced by human beings may make the concept clearer.

A person lost in a forest tends to go to the first artificial light that may be seen. Carrying out of this natural tendency illustrates a tropism even though fear might cause such a tropistic tendency to be inhibited. A young child might not tend to react positively to light until after learning to think of a light in connection with a home. The learned association of light and home would be sufficient to produce a natural tendency for definite predictable positive response.

Responses cease to be tropistic only when natural tendencies to move towards or away from stimuli are confused or completely inhibited by thought processes. Ducks that have learned to recognize water respond to it tropistically. Their response to water may be possibly tropistic the first time they see it. On the other hand, a person who refuses to go swimming because of fear of punishment or because of desires to do other things is not reacting to water in a tropistic manner. His action is not a response to water but a positive reaction to fears or desires related to other factors than water. Refusal to go into water as a result of fear of water has all the essential aspects of a tropism.

"A tropism is most effectively defined as an oriented movement in an energy field" (Crozier 1928, p. 214; Barnes 1937, p. 338). Misconceptions of tropisms are pointed out by Crozier (1928, p. 214) and Warden *et al.* (1940). Taxes such as phototaxis amount to directed locomotion. Normally, each species of animal orients towards or away from stimuli by orienting its front, side, or back to stimuli. So, taxes and kineses are normally tropisms at least in part, and for the sake of brevity may be referred to as "tropisms" since tropisms are always involved. Reversal in taxis movement does not always involve reversal of the part of the body that faces a stimulus. An animal may orient towards a stimulus and move away from the stimulus at the same moment—a negative tropism from the standpoint of total movement (*cf.* Barnes 1937, p. 339).

"Loeb's approach to the problem of individual organic behavior (1918) was initially and primarily philosophic, in the sense that through recognition of the elements of action and the modes of their control, he looked to find an answer to the puzzles of free will and determinism. With the insight permitted to a superbly penetrating intelligence, he was able to see beyond the immediate consequences of relatively simple experiments and to extract from them their utmost general significance. A quantitative treatment of tropistic behavior is essential if the understanding of conduct is to be furthered in this way. It is curious and noteworthy, however, that very seldom do current general discussions of the tropism situation appear to realize the significance of the

quantitative aspects of behavior" (Crozier 1928, p. 213).

The tropism theory for orientation of bilateral animals as presented by Loeb cannot explain orientation mechanisms of all animals (Warden *et al.* 1940). This is not a fault with the theory since Loeb was especially concerned with one type of orientation mechanism and did not believe that "deflected nervous mechanisms should account for all orientations." This is obvious since Loeb considered tropistic behavior of protozoa as well as tropistic actions of arthropods.

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FORESTS OF THE CUMBERLAND MOUNTAINS[1]

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FORESTS OF THE CUMBERLAND MOUNTAINS

INTRODUCTION

Mixed deciduous forest covers (or originally covered) almost all of the higher mountain section of southeastern Kentucky. This part of Kentucky, and smaller areas adjacent in Virginia and to the southwest in Tennessee comprise the Cumberland Mountains physiographic section, at the southeastern margin of the Appalachian Plateaus province. This is a strip nearly 150 miles long in a northeast-southwest direction, from about the Breaks of Sandy on Russell Fork of the Big Sandy River at the Kentucky-Virginia line, southwestward into Tennessee (see map, Fig. 1). The highest and most characteristic part is carved from a large block fault with more or less upturned edges which form the monoclinal mountains bordering this section—Pine Mountain along the northwest side and Cumberland and Stone Mountains on the southeast. The interior strongly dissected part, the syncline, includes Black Mountain and Little Black Mountain, the Log Mountains near Middlesboro, and other lesser mountains. The western (or northwestern) limits are fairly distinct in the northern half of the section where Pine Mountain prominently overlooks the adjacent Cumberland Plateau. Southward, the strongly dissected plateau rises to elevations approximately equal to those of the fault block mountains to the east, thus obscuring the structural limits. This higher exterior section may be included in the Cumberland Mountains.[2] In Kentucky, the boundary begins to diverge slightly from Pine Mountain south of Whitesburg, then swings westward from Pine Mountain between the Kentucky and Cumberland River drainage to about Williamsburg, including "Williamsburg Mountain" and "Jellico Mountain." The northeastern boundary of the Cumberland Mountains (from east of Norton to the Breaks of Sandy) is rather indefinite; there the Cumberlands merge into the high dissected plateau. The boundary between this northeastern part of the Cumberlands (and adjacent plateau) and the Ridge and Valley Province is, however, very pronounced.

Because of the structural features of the area and its physiographic history, a great variety of topographic situations and hence of habitats are included. Longitudinal streams have cut deep valleys paralleling the main structural features; most important of these is the Cumberland River and its major tributaries, Poor Fork, Martins Fork and Yellow Creek, and on the east side, Pound and Powell Rivers. Into these flow short lateral tributaries with steep gradients, streams which indent the mountain slopes, some forming broad and shallow coves, others, deep and narrow gorges. Such detail depends to a con-

siderable extent upon the nature of the rock which is cut (and its dip); it affects the composition of the occupying forest. The strata of Cumberland and Stone Mountains on the one side, and of Pine Mountain on the other side, are dipping; those of the central mountain masses (Black and Log Mountains) and of the outlying section are nearly horizontal. The whole area, then, is a complex of mountains carved by erosion from horizontal strata (as Black and Log Mountains) and from more or less strongly dipping strata (Pine and Cumberland Mountains); of valleys worn down on weaker rocks between the principal mountains, valleys in which there are incipient floodplains and valley flats (Cumberland valley and its major tributaries); of short tributary valleys of steep gradient indenting the mountain slopes. Elevations range from about 1,000 feet along the Cumberland River near Pineville, 1,200 feet at Harlan, and 1,700 feet near Eolia in the upper Cumberland valley, to 3,100 feet on the Log Mountains, 3,000 to 3,400 on Cumberland Mountain, 2,500 to 3,000 or over on Pine Mountain (3,200 feet at High Rock), and up to 4,250 feet on Black Mountain at the Doubles in Harlan County (indicated by Δ on map, Fig. 1).

The underlying rocks of the area all belong to the Pottsville series of the Pennsylvanian, with the exception of small areas along or near the Pine Mountain fault where older strata may be exposed. Limestone outcrops midway on the northwesterly slope of Pine Mountain and along the valleys bordering the area on the east. Elsewhere are sandstones and shales, and interbedded coal seams.

In valleys, and on the slopes of the mountains where the underlying rock is horizontal, is a deep soil mantle in most places scarcely or not at all reflecting the character of the underlying rock. Such soils generally are graybrownerths, the zonal soil type for the latitude. The humus layer is mull. Where sandstones outcrop on ridge crests or on the dip slope of Pine Mountain or of Cumberland Mountain, shallow sandy soils prevail, generally with a thin covering of mor (duff). Such soils are immature, and pronounced departure from the climatic vegetation type is seen.

No adequate picture of the climate of the area may be had from available weather data. Weather stations are few, and records have, with few exceptions, been kept but a short time. Middlesboro (with record for 40 years) would appear to be representative if one judged from its location within the area; however, the 51 inches annual precipitation there recorded gives no idea of what the rainfall on the Log Mountains but a few miles away and about 2,000 feet higher may be. On many a summer day when there is *no* rain at Middlesboro there is heavy rain on the mountains, sometimes even enough to

[2] The term "Cumberlands" is often popularly used to include the entire Cumberland Plateau. The limits used in this paper are essentially those of the Cumberland Mountains physiographic section as defined by Fenneman, 1938.
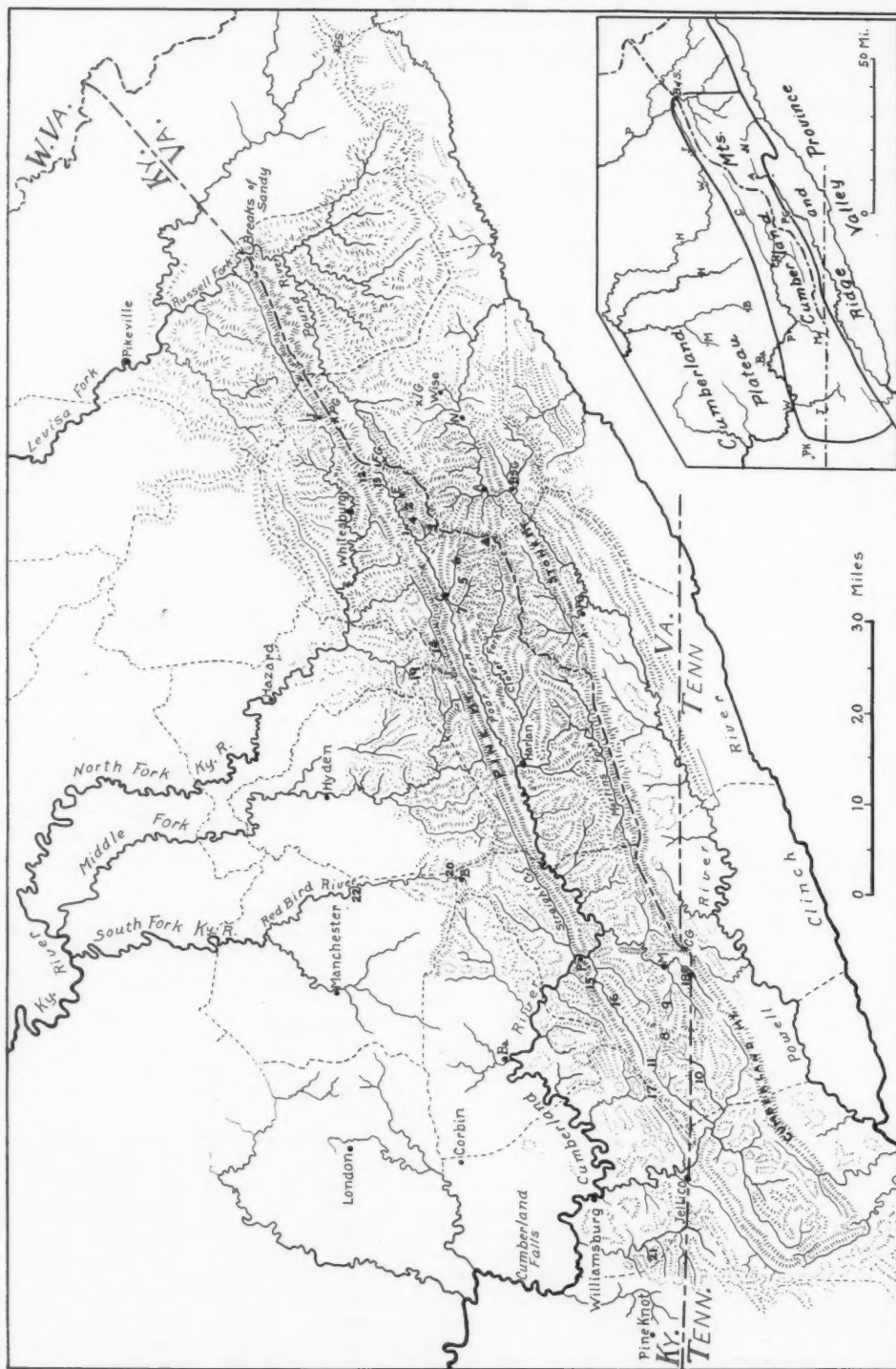
FIG. 1. Map of Cumberland Mountains and adjacent area. Inset map shows boundaries of physiographic provinces (after Fenneman). Δ—The Doubles, 4,250 ft.; FG—Pound Gap; PG—Flat Gap; IG—Indian Gap; GS—Gap of Sandy; CG—Cumberland Gap; A—Appalachia; B—Beverly; Ba—Barbourville; BSG—Big Stone Gap; C—Cumberland; E—Eolia; J—Jenkins; M—Middlesboro; N—Norton; P—Pineville (and Pine Gap); PG—Pennington Gap. Numbers refer to locations mentioned in the text.

FIG. 2. A. Mean monthly precipitation at Middlesboro. B. Mean monthly precipitation at Williamsburg. C. Mean monthly temperature at Middlesboro.

ferences in topography, elevation and soils and portray in greater or less degree the influence of these factors.

The extent of the area included here for consideration is not determined alone by physiographic boundaries, but also by vegetation. There are differences in complexity and luxuriance which affect the aspect of the forests of the Cumberland Mountains and adjacent Cumberland Plateau. Eastward, the transition to the Ridge and Valley Province is in places as sharp as the physiographic boundary. Agricultural utilization, because of fertile limestone soils in many of the valleys, accentuates the change in aspect.

The vegetation of the major topographic areas of the Cumberland Mountains will be considered separately.

The rapid decimation of forests due to recent increase in logging operations impels the writer to make available data on forest composition, for it is a matter of but very few years before no more can be obtained. Most of the area described by Braun (1940) in "An ecological transect of Black Mountain, Kentucky," has since been logged. Most of the areas for which percentage composition of canopy is given in this paper are no longer uncut; this is noted in each case. Virgin forest of any extent is all but gone. The present paper is extensive rather than intensive. It includes observations made during ten field seasons, comprising over twenty weeks in the field.[3] Although there are sections in the 5,000 or more square miles included in the Cumberland Mountains which were not visited, most of the area was traversed. The examples used for illustration are selected from the best and most representative areas. The emphasis throughout is on *original* forest. The desirability of more detailed statistical studies than are included here is recognized; the extent of the area and the inaccessibility of the best sites (and later their destruction) precluded this. Frequent visits to places 5 or 10 miles from any highway are difficult; when highways came, the forest went.

THE CENTRAL MOUNTAIN AREA: BLACK MOUNTAIN AND LOG MOUNTAINS

The dominant feature of both Black and Log Mountains is the splendid mixed deciduous forest of the mountain slopes. Apparently the whole synclinal area is mixed forest, for here where underlying strata are horizontal there is generally deep soil, in contrast to the shallow soil over the dipping strata of the bordering mountains. Composition of the forest varies in relation to slope exposure and, to some extent, to altitude. On southerly exposures, especially at low elevations, white oak and beech are numerically most important; on narrow ridge crests or very steep south or southwesterly slopes, some variant of an oak-chestnut community may prevail; elsewhere the mixed mesophytic forest in which bass-

bring streams out of their banks. As all stations in or at the borders of the Cumberland Mountains are in valleys, the data compiled in Figure 2, for Middlesboro and Williamsburg, are suggestive only. Middlesboro, at an elevation of 1,128 feet, has average annual precipitation of 50.92 inches; average annual temperature, 57° F.; highest and lowest recorded temperatures, 112° and —20° F.; average minimum for January, 27.5° F.; average maximum for July, 87.2° F.; frostless season, April 18 to October 18. Williamsburg, elevation 939 feet, has average annual precipitation of 49.12 inches; average annual temperature, 56.8° F.; highest and lowest recorded temperatures, 105° and —19° F.; average minimum for January, 27.3°; average maximum for July, 89°; frostless season, April 17 to October 21.

VEGETATION

The deciduous forest of the Cumberland Mountains is outstanding in its superlative quality. In number of tree species, in size of individuals, in variety of forest types it ranks as one of the finest deciduous forest areas of North America. The mixed mesophytic forest association is here at its best; nowhere else is it as well developed (Braun 1941). Variations in forest composition are related to dif-

wood, sugar maple, tulip tree, buckeye, beech, chest-
nut, and red oak are most abundant is seen. Even
on south slopes, unless convex, or at very low eleva-
tion, enough of the characteristic trees of the mixed
mesophytic forest occur to give a decidedly mixed
aspect. This is most strikingly seen during the period
of fall coloration when the great number of species
of the mixed forest assume different hues. Then, the
small area occupied by the oak-chestnut forest is
most apparent.

Some altitudinal sequence of forest types is dis-
cernible. Beech and white oak may be numerically
important constituents of forest communities at eleva-
tions below about 2,000 feet. Above this elevation
they are absent (except that they reappear at nearly
4,000 feet), and other constituents of the mixed
mesophytic forest, especially basswood, buckeye,
sugar maple, and tulip tree, are proportionately more
abundant. Above 2,000 feet, sugar maple becomes
increasingly abundant (Fig. 8). At elevations of
about 3,700 feet, the admixture of birch and cherry
and the reappearance of beech, introduce a new for-
est aspect. This may be seen only on the highest
slopes of Black Mountain (Fig. 7).

Studies made in various parts of the mountains
serve to demonstrate the variations in type of forest
developing in different habitats. The central moun-
tain area may be divided conveniently into two sec-

tions, separated by the north-south line connecting
Pineville (or Pine Gap in Pine Mountain) and
Cumberland Gap (see map, Fig. 1). To the north-
east are the Black Mountains of which Black Moun-
tain and Little Black Mountain are most important
(Fig. 3). To the west are the Log Mountains (Fig.
11).

BLACK MOUNTAIN

In a previous paper, most of the forest communi-
ties of Black Mountain have been considered (Braun
1940). There remain, however, a few distinct com-
munities poorly or not at all represented in the area
there treated (those of lowest and of highest slopes)
and certain areas of lesser importance, topographi-
cally young, and hence vegetationally different.

Forests of Low Elevations

On southerly slopes (southeast to southwest), a
beech-white oak forest type prevails. This generally
is poorly preserved, for it is adjacent to cleared and
farmed valleys; its white oak generally was cut for
farm buildings or for mine props; it now is often
overrun with hogs. There are remnants, however,
which clearly indicate the widespread occurrence in
suitable habitats of this forest type, a type consid-
ered in greater detail in connection with the vegeta-
tion of the "Monoclinal Borders," where, on the slopes

FIG. 3. View of Black Mountain from Pine Mountain about ten miles above Cumberland. Pines in fore-
ground on a sandstone outcrop; the valley indenting the slopes of Black Mountain is that of Colliers Creek.

of Limestone Creek (location 17 on map, Fig. 1) good examples remain and in the "Vegetation of Pine Mountain" (Braun 1935), along Line Fork on slopes opposing Pine Mountain (location 14 on map). In places beech is dominant, and Rhododendron and Kalmia form a lower layer. This variant, which appears on the lower slopes of Benham Spur, may be related to a sandstone horizon.

White oak is abundant at the lower elevations not only in the white oak-beech type of warmer slopes, but also in ravine and cove forests with hemlock. This is well illustrated in the lower part of the valley of Colliers Creek in Letcher County.

Lower elevation cove forest; hemlock and white oak abundant; Colliers Creek, Letcher County.

	Percent
Tsuga canadensis, hemlock	42
Quercus alba, white oak	28
Acer rubrum, red maple	11
Quercus borealis maxima, northern red oak	6
Fagus grandifolia, beech	5
Magnolia Fraseri, mountain magnolia	3
Aesculus octandra, buckeye	2
Castanea dentata, chestnut	2
Betula alleghaniensis,[4] birch	1

Mixed mesophytic forest of lower elevations of valleys; white oak one of the important species; Colliers Creek.

	Percent
Liriodendron tulipifera, tulip tree	17
Fagus grandifolia, beech	16
Castanea dentata, chestnut	16
Tsuga canadensis, hemlock	13
Acer rubrum, red maple	10
Quercus alba, white oak	7
Quercus borealis maxima, northern red oak	5
Juglans nigra, walnut	3
Juglans cinerea, butternut	3
Nyssa sylvatica, sour gum	3
Magnolia Fraseri, mountain magnolia	3
Betula alleghaniensis, birch	2
Aesculus octandra, buckeye	1
Carya sp., hickory	1

In the first of these examples, white oak is an important constituent in the cove hemlock forest, where the great density of canopy almost eliminates ground vegetation. In the second, it is one of the important constituents of the mixed mesophytic forest of the lower elevations of valleys on the slopes of Black Mountain.[5]

On northerly slopes, at low elevations, white oak is absent; beech is proportionately more abundant, generally constituting about 50 percent of a forest in which several other mesophytes make up most of the rest of the canopy. In one place, on lower north slopes in Cave Branch of Cloverlick Creek (location 7 on map), sugar maple is second in abundance to beech, although certainly not of sufficient abundance to be thought of as codominant with the beech. This is the only place seen in the entire Cumberland

Mountains in which there is any approach toward what could be termed a beech-maple forest.

Forest of Cave Branch of Cloverlick Creek, Harlan County.

	Percent
Fagus grandifolia, beech	50
Acer saccharum, sugar maple	16
Liriodendron tulipifera, tulip tree	10
Tilia heterophylla, basswood	8
Aesculus octandra, buckeye	5
Castanea dentata, chestnut	5
Magnolia acuminata, cucumber tree	⎫
Betula alleghaniensis, birch	
Betula lutea, yellow birch	⎬ 6
Carya sp., hickory	
Nyssa sylvatica, sour gum	⎭

Many constituents of the mixed forest are present, including the highly characteristic *Tilia heterophylla* and *Aesculus octandra*, and in both canopy and understory there are species of southerly range. The herbaceous layer of this forest is the rich and varied sort with an abundance of ferns, which is found in all good areas of mixed mesophytic forest.

In secondary areas at lower elevations, white oak is often very prominent on southerly slopes. Tulip tree generally forms pure stands on northerly and easterly slopes, unless erosion has been active.

Forests of High Elevations

The highest elevation in the Cumberland Mountains, 4,250 feet, is reached at the Doubles on Black Mountain in Harlan County (△ on map, Fig. 1). At these highest elevations, the admixture of birch gives a different aspect to the forest. Topographic situation—flat or narrow ridge top, or slope—and direction of slope greatly affect the composition of forest canopy and understory. (For composition of summit types, other than those of highest elevations, see Braun 1940, p. 229, Fig. 20.)

The summit forest was[6] prevailingly oak-chestnut, with *Castanea dentata*, *Quercus borealis maxima*, and *Quercus montana* the dominant trees (Fig. 4). Red oak is much more abundant in this summit oak-chestnut forest than in the oak-chestnut of lower elevations. It reaches larger size than other trees of the summit forest, sometimes 4 feet or more in diameter. Locally, sugar maple, birch, cucumber, red maple, and occasional beech were also present. Parts of this summit oak-chestnut forest had a prominent heath layer with the evergreen *Kalmia latifolia* abun-

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[4] It is possible that some *B. lenta* is included; however, those trees of which fruiting branches were obtained are best referred to *B. alleghaniensis* on a basis of fruit-bract characters.

[5] This is somewhat comparable to area I of the ravine slopes of Joe Day Branch, previously considered, *loc. cit.*, 1940, p. 209.

[6] The word "was" is used intentionally. When the area was first visited in August, 1931, there was no indication of disturbance of any sort. The chestnut blight was not apparent. The next year, its presence was noted, and by 1935, when the area was next visited, all the chestnut was about dead. Then, the dead chestnut was cut out. The added light reaching lower layers of the forest was soon reflected in vigorous growth of chestnut sprouts, of young chestnut oak, and other saplings, and in many places of blackberries. The aspect was greatly changed, for instead of the rather open growth of reproduction and luxuriant shrub and herbaceous layers, there came to be a dense low woody growth which greatly crowded the forest shrubs and herbs. Recently, the entire area has been logged. Hence no high elevation forest remains. For this reason, more details concerning lower layers of these summit and upper slope forests is given than for other Black Mountain areas treated in this paper. The dominance of the three tree species mentioned was so obvious, that unfortunately no counts were made from which to determine actual percentage composition of canopy.

FIG. 4. Oak-chestnut forest of summit of Black Mountain near the Doubles. Photograph taken Oct. 6, 1931, before blight affected chestnut.

FIG. 5. Red azalea (in bloom) and cinnamon fern in oak-chestnut forest of summit of Black Mountain near the Doubles. June 30, 1932.

dant; in places was a dense shrub layer in which the deciduous heaths, *Vaccinium pallidum*, *V. simulatum*, and especially the red azalea *(Rhododendron cumberlandense)*[7] prevailed, along with other shrubs and understory trees (Fig. 5). Elsewhere, there was no shrub layer, although of course scattered shrubs were present. In places, particularly on spur ridges, a massive sandstone outcrops; this locally affects the vegetation.

Shrubs and small tree species of the summit forest are:

Pyrularia pubera	*Kalmia latifolia*
Hydrangea arborescens	*Rhododendron*
Hamamelis virginiana	*cumberlandense*
Amelanchier canadensis	*Rhododendron maximum*
Amelanchier laevis	*Vaccinium pallidum*
Crataegus macrosperma	*Vaccinium simulatum*
Rubus canadensis	*Sambucus racemosus*
Ilex monticola	*Viburnum acerifolium*
Acer pennsylvanicum	

The herbaceous layer contains a large number of species, some of which are generally distributed, others very local. The spring (late May) aspect of the summit was emphasized by the many flowers of which *Geranium maculatum* and *Ranunculus hispidus* are very abundant. Later the abundance of cinnamon fern *(Osmunda cinnamomea)* is striking (Fig. 5). Locally, in or near heath areas, *Trillium undulatum* is found.

Herbaceous plants of the summit oak-chestnut forest are:

Aspidium marginale	*Cypripedium parviflorum*
Aspidium noveboracense	var. *pubescens*
Aspidium spinulosum	*Stellaria pubera*
Asplenium acrostichoides	*Anemone lancifolia*
Asplenium angustum	*Cimicifuga americana*
Dicksonia punctilobula	*Cimicifuga racemosa*
Osmunda cinnamomea	*Clematis viorna*
Osmunda Claytoniana	*Ranunculus abortivus*
Polystichum	*Ranunculus hispidus*
acrostichoides	*Ranunculus recurvatus*
Pteris aquilina	*Thalictrum dioicum*
Agrostis perennans	*Caulophyllum*
Panicum latifolium	*thalictroides*
Poa cuspidata	*Podophyllum peltatum*
Carex aestivalis	*Sanguinaria canadensis*
Carex alleghaniensis	*Dentaria laciniata*
Arisaema triphyllum	*Sedum ternatum*
Clintonia umbellulata	*Aruncus sylvester*
Disporum lanuginosum	*Amphicarpa monoica*
Erythronium americanum	*Geranium maculatum*
Lilium canadense	*Impatiens pallida*
Lilium superbum	*Hypericum*
Medeola virginiana	*pseudomaculatum*
Smilacina racemosa	*Viola blanda*
Smilax herbacea	*Viola canadensis*
Trillium erectum	*Viola emarginata*
Trillium grandiflorum	*acutiloba*
Trillium undulatum	*Viola hastata*
Uvularia perfoliata	*Viola palmata*
Cypripedium acaule	*Viola rotundifolia*

Viola scabriuscula	*Pedicularis canadensis*
Aralia racemosa	*Conopholis americana*
Angelica Curtisii	*Houstonia purpurea*
Thaspium aureum	*Campanula divaricata*
atropurpureum	*Lobelia inflata*
Lysimachia quadrifolia	*Aster cordifolius*
Steironema intermedia	*Aster divaricatus*
Gentiana decora	*Eupatorium purpureum*
Asclepias phytolaccoides	*Eupatorium urticaefolium*
Hydrophyllum virginianum	*Helianthus microcephalus*
Monarda clinopodia	*Solidago Curtisii*

The oak-chestnut summit forest extended a short distance down southwesterly slopes (toward head of Clover Fork) before giving way to the mixed forest of upper slopes.

                                               Percent

Castanea dentata	47
Quercus borealis maxima	21
Magnolia acuminata	11
Acer rubrum	7
Quercus alba	6
Nyssa sylvatica	3
Fagus grandifolia	3
Betula alleghaniensis	2

In the understory were the same species (again with red oak and chestnut most abundant) and wild cherry *(Prunus serotina)* and sourwood *(Oxydendrum arboreum)*, the former of which happened to be lacking in the canopy in this area. Slightly lower, the aspect becomes more mesophytic, although the forest is very similar. Beech is generally a constituent of this forest.

On northerly slopes, at the head of Looney Creek (location 6 on map), a mixed mesophytic forest in which sugar maple is abundant ascends to the summit (Fig. 6). Here birch is also a frequent constituent of the forest (Fig. 7). The admixture of black cherry suggests the approach here to the altitudinal band in the Great Smoky Mountains in which cherry is so important as to be referred to locally as the "cherry orchards."

                                              Percent

Acer saccharum	46
Betula alleghaniensis	18
Aesculus octandra	7
Tilia heterophylla	6
Castanea dentata	6
Fagus grandifolia	4
Prunus serotina	3
Quercus borealis maxima	3
Fraxinus americana	2
Acer rubrum	2
Magnolia acuminata	2

This upper north slope forest was a magnificent forest of large trees, many reaching heights well over 100 feet and trunk diameters of 3 or 4 feet.[8] Tree branches above about 50 feet are covered with lichens, especially conspicuous being *Usnea barbata*. This reflects the influence of the band of mist which

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[7] The azalea referred to in previous papers (Braun 1935, 1940) as "red azalea" has since been described as *Rhododendron cumberlandense* (Braun 1941a).

[8] A fallen ash 40 inches d.b.h. was measured which was 70 feet to the first small branch, and 100 feet to where the trunk gave off the first large branches; a fallen birch measured 100 feet from base into small branches.

FIG. 6. View of Black Mountain at the head of Looney Creek. All slopes covered with mixed mesophytic forest. The open appearance of the forest along the skyline is due to season; the oaks and chestnut of the summit forest at 4,000 ft. have not come into leaf, although the slope forests are in full leaf. May 24, 1932.

FIG. 7. Forest of the north slope at the head of Looney Creek. The nearer trees are birch. May 23, 1932.

frequently hangs about the upper mountain slopes. A luxuriant and beautiful herbaceous layer, in which are included a few northern and high Alleghenian species, helped to make this one of Black Mountain's most beautiful forests. Here was the only known Kentucky station for *Streptopus roseus* var. *perspectus.* This herbaceous layer included:

Adiantum pedatum　　　　*Aspidium spinulosum*
Aspidium noveboracense　*Asplenium acrostichoides*

*Phegopteris
　hexagonoptera*
Arisaema triphyllum
Allium tricoccum
Disporum lanuginosum
Disporum maculatum
Erythronium americanum
Medeola virginiana
Melanthium parviflorum
Smilacina racemosa
*Streptopus roseus
　perspectus*
Trillium erectum
Trillium grandiflorum
Habenaria psycodes
Orchis spectabilis
Laportea canadensis
Asarum canadense
Stellaria pubera
Actaea alba
Anemone quinquefolia

Delphinium tricorne
Hepatica acutiloba
*Caulophyllum
　thalictroides*
Podophyllum peltatum
Dicentra canadensis
Dentaria diphylla
Dentaria laciniata
Mitella diphylla
Tiarella cordifolia
Oxalis montana
Impatiens pallida
Viola affinis
Viola blanda
Viola canadensis
Viola scabriuscula
Osmorhiza longistylis
Hydrophyllum virginianum
Collinsonia canadensis
Monarda clinopodia

The dominance of plants belonging in a mull humus layer is evident.

With only slight variations, this forest extends down to the sugar maple-basswood-buckeye forest which is so predominant at middle elevations in the Cumberland Mountains (see forest of Joe Day Branch, Black Mountain, *loc. cit.,* pp. 212, 213; location 2 on map, Fig. 1 of this paper).

Transition to sugar maple-basswood-buckeye forest, near summit at head of Rogers Fork of Colliers Creek (location 3 on map).

	Percent
Acer saccharum	40
Tilia heterophylla	19
Quercus borealis maxima	13
Aesculus octandra	7
Prunus serotina	7
Castanea dentata	7
Betula allegheniensis	3
Magnolia acuminata	3
Fraxinus americana	1

Typical sugar maple-basswood-buckeye forest, Colliers Creek.

	Percent
Acer saccharum	36
Aesculus octandra	25
Tilia heterophylla	23
Liriodendron tulipifera	4
Carya sp.	3
Fraxinus americana	3
Quercus borealis maxima	2
Castanea dentata	
Magnolia acuminata	
Juglans cinerea	4
Juglans nigra	
Betula allegheniensis	
Magnolia Fraseri	

FIG. 8. Sugar maple is dominant in this forest on the upper slopes of Black Mountain near the head of Colliers Creek. May 4, 1934.

FIG. 9. Sugar maple-basswood-buckeye forest of middle elevations on Black Mountain, near the head of Colliers Creek. Large sugar maple to right, tulip tree to left, and buckeye and sugar maple beyond. May 4, 1934.

The aspect of the transition forest, in which sugar maple may be dominant, and of the sugar maple-basswood-buckeye forest is illustrated by Figures 8, 9 and 10.

River Bluffs

As a result of lateral planation, spurs of Black Mountain are in places truncated, and a topographically young habitat produced. Where actual cliffs are formed, various rock plants occur. Even the steepest slopes, if a little soil has accumulated, support an assemblage of tree species—usually young individuals—indicating the early establishment of mixed mesophytic forest. Hemlock is generally a constituent of the forest of these truncated faces. Where more massive rock is exposed, heath shrubs are conspicuous.

LOG MOUNTAINS

To the west of Middlesboro the Log Mountains rise to elevations a little over 3,000 feet (Fig. 11). As on Black Mountain, some phase of mixed mesophytic forest prevails except on the most xeric situations. The highest altitude types of Black Mountain are lacking, the sugar maple-basswood-buckeye type extends almost to the top on mesic slopes. Locally, red oak is abundant, especially at the highest eleva-

Fig. 10. Basswood and sugar maple in the sugar maple-basswood-buckeye forest on Black Mountain near the head of Colliers Creek.

Fig. 11. View of the Log Mountains with the cleared valley of Laurel Fork in the foreground. The forest areas represented by chart, Figure 12, are on the upper slopes.

tions where it mixes with the sugar maple-basswood-buckeye forest and with the chestnut of the summit ridges, and on mesic southerly slopes above about 2,500 feet. The accompanying chart, Figure 12, is designed to show the shift in dominance with changing slope exposure, and the abundance of white oak and beech on south slopes (7 of chart) at slightly lower elevations (location 8 on map, Fig. 1).

In luxuriance of herbaceous layer the mixed mesophytic forest of the Log Mountains is comparable to that of Black Mountain. Apparent exceptions are due to the rooting by hogs, which in many sections of the mountains have roamed more or less at will for perhaps a century or more. Where the herbaceous layer appears poor, if a habitation is near (within a half-mile or a mile), and if there is no "hog law" which requires confinement of these animals, hogs are the cause.

The forest of the lower mountain slopes is, on the drier southern exposures, the beech-white oak type (seen along the slopes of Yellow Creek, location 9, and of Clear Fork, location 10). On more mesic

lower slopes is a more typical mixed mesophytic association with beech, white oak, sugar maple, basswood, buckeye, tulip tree, and a sprinkling of other species. Wherever white oak becomes abundant, basswood is less prominent.

On lower northerly exposures, where slopes are very gentle, beech may be dominant and the aspect approach that of the beech consociation of valley flats which is of frequent occurrence in the area of the mixed mesophytic forest. A forest in Laurel Fork (location 11 on map) is of this type (Fig. 13).

Percent

Fagus grandifolia	58
Quercus alba	9
Liriodendron tulipifera	8
Acer rubrum	7
Castanea dentata	6
Nyssa sylvatica	5
Tilia heterophylla	
Tsuga canadensis	
Quercus borealis maxima	7
Acer saccharum	
Magnolia acuminata	
Carya ovata	

Rhododendron maximum is prominent near the streams. In some ravines, hemlock is abundant; its occurrence bears little or no relation to slope exposure.

In general the forest of the Log Mountains, like that of Black Mountain, is mixed mesophytic throughout, except as interrupted by tongues of oak-chestnut forest on the driest ridges. The mixed mesophytic forest with beech prevails at lower elevations; higher, the sugar maple-basswood-buckeye type prevails.

The Monoclinal Borders: Pine, Cumberland, and Stone Mountains

The most striking feature of the inner (dip) slopes of Pine and Cumberland Mountains is the large amount of pine in some parts of the forest. This interruption to the prevailing deciduous forest is correlated with shallow sandy soils overlying the dipping sandstone strata. Pine is more conspicuous on Pine Mountain, where the direction of the dip slope is southeast, than on Cumberland Mountain, where the northwesterly direction of the slope to a slight extent offsets the effect of shallow soils. Wherever deeper soils accumulate, deciduous forest dominates.

The steeper scarp slopes of both these mountains, the northwest slope of Pine Mountain, the southeast slope of Cumberland Mountain, support deciduous forest. That on Pine Mountain is of a more luxuriant type, due to the northwesterly direction of the slope which increases its mesophytism. However, the southeast slope of Cumberland Mountain appears to have been covered with mixed mesophytic forest, perhaps with a higher percentage of oaks and hickories. In contrast to the corresponding scarp slope of Pine Mountain, forests of Cumberland Mountain are almost entirely secondary, due doubtless to ease of access from the adjacent agricultural valleys.

AREA NUMBER	1	2	3	4	5	6	7
NUMBER of TREES	216	64	45	109	45	28	29
Acer saccharum							
Tilia heterophylla +							
Aesculus octandra							
Liriodendron tulipifera							
Quercus borealis maxima							
Castanea dentata							
Quercus montana							
Quercus alba							
Fagus grandifolia							
Carya spp.							
Fraxinus americana							
Magnolia acuminata							
Nyssa sylvatica							
Robinia pseudo-acacia							
Juglans nigra							
Juglans cinerea							
Prunus serotina							

Fig. 12. Percentage composition of canopy of forest communities on Log Mountains near head of Laurel Fork (location 8 on map, Fig. 1). The direction of slope shifts around the head of the valley, from north in areas 1 and 2 to south in area 7. Area 4 extends higher up the slopes than do other areas, approaching a ridge crest; area 6 illustrates a convexity of slope; area 7 is nearly 1,000 ft. lower than the upper part of area 4. (In all the charts, percentages are shown by solid black portion of square; percentages less than 5, by bars reaching a proportionate distance across the base line.)

PINE MOUNTAIN

The dip slope of Pine Mountain almost everywhere descends to longitudinal valleys skirting its southeastern base. From the valley, or from the opposing mountain sides, this slope of Pine Mountain seems to be very uniform, and more or less horizontally banded with pine and deciduous forest. However, it is deeply cut by transverse streams whose valleys in places are deep gorges, in others widen into deep pockets or even open troughs. Although such valleys open to the south, they are always well watered and their forests present astounding contrasts to the apparently continuous xeromesophytic forest of the dip slope. Many of the features of the vegetation of Pine Mountain have already been treated by the writer.[9] Additional studies south of the gap at Pineville substantiate the general features previously described and add new data. In Kentucky Ridge State Park[10] are some remarkably well preserved remnants of forests in ravines of the dip slope. It is possible, with few interruptions, to get the sequence from mountain summit down into deep hemlock gorges (location 15 on map). Minor streams here

[9] "Vegetation of Pine Mountain, Kentucky" (1935). The specific features of vegetation described in this paper are based on observations in Letcher and Harlan counties.
[10] Kentucky Ridge State Park is on Pine Mountain south of Pineville, *not* on "Kentucky Ridge" which extends north and west from Pine Mountain north of Pineville and is the divide between the Kentucky and Cumberland River drainage.

do not have longitudinal sections in troughs high on the mountain as is more generally true farther north on Pine Mountain (Braun 1935). Instead, they may follow a fairly direct course down the mountain. Near the head of such a stream, the ravine is little more than a concavity on the south slope. Lower, it cuts into the sandstone, which in places stands as almost vertical cliffs. There is a pronounced change in forest composition correlated with this change in character of the ravine, a change from oak forest to one in which hemlock is the most abundant species. Occasional forest areas of south exposure on the slopes of the ravine are comparable in composition to the forest of the ravine head. In the deeper parts of such ravines are magnificent forests, about half hemlock, with a wealth of *Rhododendron maximum*. *Stewartia pentagyna* is abundant anywhere that hemlock and Rhododendron do not prevail. One of these areas is known as "Hemlock Gardens." From the lower opposing slopes of Clear Creek (location 16 on map) none of these features are noticeable. There seems to be scarcely a break in the oak-pine slope.

A study of representative areas in the several communities distinguished illustrates the differences in canopy composition and the change from the oak-chestnut forest of the upper mountain slopes to the hemlock forest of gorges (Fig. 14). The understory

FIG. 13.   Beech forest of Laurel Fork in the Log Mountains.   June 23, 1935.

AREA NUMBER	1	2	3	4	5
NUMBER OF TREES	59	56	149	293	150
Quercus montana					
Castanea dentata		*		*	*
Carya spp.					
Nyssa sylvatica					
Quercus velutina					
Pinus echinata					
Quercus coccinea					
Oxydendrum arboreum					
Sassafras variifolium					
Magnolia macrophylla					
Juglans cinerea					
Fraxinus americana					
Magnolia acuminata					
Quercus borealis maxima					
Tilia heterophylla +					
Acer rubrum					
Betula allegh_eniensis					
Quercus alba					
Liriodendron tulipifera					
Fagus grandifolia					
Tsuga canadensis					

FIG. 14. Percentage composition of canopy of forest communities in Kentucky Ridge State Park on Pine Mountain near Pineville (location 15 on map). Illustrates change from oak-chestnut forest of upper mountain slopes to hemlock forest of gorges. Areas 1 to 4 in sequence from head of ravine down into "Hemlock Gardens"; area 5 in another nearby ravine. Asterisk in chart indicates that dead chestnut may have been removed. See also Table 1.

in all cases is similar to the canopy. The great difference between shrub and herbaceous layers of the several communities is evident from the lists (Table 1); areas 1 and 2 belong to the oak-chestnut forest and have nothing in common with the more mesophytic communities, areas 3, 4, and 5. However, these mesophytic forest communities differ strikingly in their herbaceous layer from the luxuriant mixed mesophytic forests of Black and Log Mountains (*cf.* lists, pp. 421, 422 and Braun 1940).

The "summit" of Pine Mountain is almost everywhere the broken edge of a dipping stratum which forms cliffs at the top of the scarp slope. There are no summit ridges in the same sense that these occur on Black and Log Mountains. There is, of course, variation in the sharpness of this contact between dip and scarp slopes, and there are few nearly level summit areas, generally in the vicinity of gaps (Fig. 15). Where prominent cliffs occur, there may be almost no forest vegetation along the mountain crest (as at High Rock, location 12 on map; *loc. cit.* 1935). Generally, however, there is an open oak or oak-pine forest in which the following trees may occur:

Quercus coccinea	Castanea dentata
Quercus falcata	Pinus rigida
Quercus marilandica	Pinus virginiana
Quercus montana	Carya alba
Quercus stellata	Carya glabra
Quercus velutina	Oxydendrum arboreum

Every crack in the cliffs is occupied by shrubs, most prominent of which are *Rhododendron maximum, Rhododendron catawbiense, Kalmia latifolia, Vaccinium* spp., *Gaylussacia baccata,* and in places, *Philadelphus hirsutus.* On less extreme parts of the summit, tulip tree, walnut and shell-bark hickory occur in a chestnut oak forest.

The scarp slope (northwest slope) of Pine Mountain is almost an unbroken slope, everywhere sup-

FIG. 15. Open chestnut oak forest of flat-topped part of summit of Pine Mountain about 15 miles southwest of Pineville.

TABLE 1. Undergrowth of forest communities shown in Figure 14, illustrating contrast between oak-chestnut communities of upper slopes (areas 1, 2) and ravine forests in which hemlock is a dominant (areas 3, 4, 5).

UNDERSTORY TREES, CANOPY SPECIES	1	2	3	4	5
Quercus montana	X	X	X		
Castanea dentata	X	X			
Carya spp.	X	X	X		
Nyssa sylvatica	X	X			
Quercus velutina	X				
Pinus echinata		X			
Quercus coccinea		X			
Quercus borealis maxima		X	X		X
Oxydendrum arboreum	X	X		X	X
Sassafras variifolium		X	X		
Magnolia macrophylla				X	X
Juglans cinerea					X
Fraxinus americana					X
Magnolia acuminata			X	X	X
Tilia heterophylla					X
Acer rubrum	X	X			X
Betula alleghaniensis			X	X	X
Quercus alba		X			
Liriodendron tulipifera		X	X	X	
Fagus grandifolia				X	X
Tsuga canadensis			X	X	
UNDERSTORY TREES, NOT IN CANOPY					
Robinia Pseudo-Acacia	X	X	X		
Diospyros virginiana		X			
Amelanchier canadensis		X	X		
Cornus florida		X	X	X	X
Ilex opaca			X	X	
Magnolia tripetala			X	X	X
Juglans nigra					X
Cladrastis lutea					X
SHRUBS AND WOODY CLIMBERS					
Aralia spinosa				X	X
Benzoin aestivale					X
Bignonia capreolata					X
Ceanothus americanus		X			
Clethra acuminata			X	X	X
Evonymus americanus					X
Hamamelis virginiana			X		X
Hydrangea arborescens			X		X
Kalmia latifolia		X	X	X	
Psedera quinquefolia					X
Rhododendron cumberlandense	X		X		
Rhododendron maximum			X	X	X
Rhus Toxicodendron					X
Rubus sp.			X		X
Sambucus canadensis					X
Smilax glauca	X				
Stewartia pentagyna			X	X	X
Vaccinium sp.	X	X			
Vaccinium stamineum	X	X	X		
Vaccinium vacillans	X	X	X		
Viburnum acerifolium					X
Vitis aestivalis		X			
Vitis bicolor			X		
GROUND HEATHS					
Chimaphila maculata			X		X
Epigaea repens	X		X		
Gaultheria procumbens			X		
Galax aphylla	X		X	X	

FERNS	1	2	3	4	5
Adiantum pedatum				X	
Aspidium noveboracense			X	X	X
Aspidium marginale			X		X
Aspidium spinulosum			X		X
Asplenium acrostichoides					X
Asplenium angustum				X	X
Dicksonia punctilobula				X	X
Osmunda cinnamomea				X	X
Phegopteris hexagonoptera					X
Polypodium virginianum			X	X	
Polystichum acrostichoides			X	X	X
Pteris aquilina	X				
HERBS					
Andropogon scoparius	X				
Panicum spp.		X			
Sorghastrum nutans	X				
Arisaema quinatum					X
Arisaema triphyllum			X	X	X
Aletris farinosa	X				
Clintonia umbellulata			X		X
Disporum lanuginosum					X
Medeola virginiana			X	X	X
Trillium erectum					X
Dioscorea quaternata			X		
Iris cristata			X	X	
Calopogon pulchellus			X		
Cypripedium acaule				X	X
Epipactis pubescens			X		
Microstylis unifolia			X		
Laportea canadensis					X
Pilea pumila				X	X
Asarum arifolium				X	X
Stellaria pubera				X	
Actaea alba					X
Clematis virginiana			X		
Ranunculus recurvatus					X
Corydalis sempervirens			X		
Heuchera longiflora			X		
Tiarella cordifolia					X
Desmodium nudiflorum	X				
Desmodium pauciflorum			X		
Lespedeza spp.	X	X			
Oxalis montana			X		
Euphorbia corollata	X				
Viola blanda			X	X	X
Viola hastata				X	X
Viola rotundifolia			X	X	X
Circaea lutetiana					X
Aralia racemosa			X		
Panax quinquefolium					X
Osmorhiza longistylis					X
Gerardia laevigata	X				
Houstonia tenuifolia	X				
Mitchella repens			X	X	X
Antennaria plantaginifolia		X			
Aster divaricatus			X	X	X
Aster surculosus	X				
Brachychaeta sphacelata	X				
Chrysopsis graminifolia	X				
Chrysopsis mariana		X			
Elephantopus tomentosus	X				
Eupatorium purpureum					X
Eupatorium urticaefolium					X
Helianthus sp.		X			
Solidago caesia			X		
Solidago odora	X				

porting mixed mesophytic forest. Occasional low limestone cliffs may slightly interrupt this forest. Such breaks are unimportant, although the limestone cliffs do afford local habitats for a variety of plants not found within the forest. If not too steep, the limestone bench is cultivated, and occupied by patches of corn.

Longitudinal creeks generally skirt the northwest base of Pine Mountain and between their headwaters mountain spurs extend out connecting Pine Mountain with adjacent irregular ridges. In the south these ridges are as high or almost as high as Pine Mountain and merge into the extensive exterior section to the west. Near the southern border of Kentucky on Pine Mountain, studies were made on the northwest slope of Pine Mountain and the opposing southeast slopes across Limestone Creek (location 17 on map). Here in absolutely unbroken forest, the entire sequence on both slopes was available.[11]

Viewed from the summit of Pine Mountain (Fig. 16) the forest appears to be entirely mixed mesophytic, except for small patches of pine on cliffs of the opposite mountain face (south slope). Variations in relation to slope exposure and topography are

[11] Much cutting has since been done, and a limestone quarry for road material opened up, where in 1935 there was virgin forest.

seen, notably the higher proportion of oaks and absence of basswood (except very low) on the south slope; the large amount of beech in the valley of Limestone Creek and extending a short distance up *both* slopes; the abundance of tulip tree on both slopes; the prevalence of the sugar maple-basswood-buckeye-tulip tree forest over much of the northwest slope; and the admixture of chestnut almost throughout the forest.

On the Pine Mountain slope, the change from beech dominance on the lower slope, to the sugar maple-basswood-tulip tree association-segregate of the mixed mesophytic forest (Fig. 17) which continues almost to the top, is clearly shown. Tulip tree is an important constituent of the higher part of this community (Fig. 18). On the upper slopes, the greater abundance of chestnut may be noted. The sequence of communities encountered from base to summit on the northwest slope, and from wide ravine floor to headwaters along the longitudinal stream at the base of the mountain are closely comparable (see chart, Fig. 19). It should be noted that the sugar maple-basswood-buckeye-tulip tree forest is here at a lower elevation (1,500-2,000 feet) than it usually occurs on Black or Log Mountain. This entire area of mixed mesophytic forest was a forest striking in the large number of tree species

FIG. 16. View northwest from Pine Mountain (on the Bell-Whitley County line at location 17 on map), showing a portion of the high dissected area of the Cumberland Mountains west of Pine Mountain.

FIG. 17. In the sugar maple-basswood-buckeye community of the northwest slope of Pine Mountain above Limestone Creek (area III of chart, Fig. 19). The large tree is buckeye *(Aesculus octandra)*, with papaw *(Asimina triloba)* at its base.

it contained, and the large size attained by many of the individuals.[12]

The herbaceous layer is the luxuriant type so prevalent in the Cumberland Mountains. There is no rhododendron in the valley (probably a reflection of the limestone substratum for which the creek is named), and almost no hemlock. A slight influence of the limestone is seen in the specific content of lower layers.

The forest of the opposing south or southeast slopes (Fig. 20) lacks the luxuriant aspect of the herbaceous layer. The greater proportion of oak increases the exposure to sunlight in spring (due to late leafing of oak), affects the nature of the humus, and hence affects herbaceous growth. Fewer ferns, more legumes (Desmodium and Lespedeza), more xeromesophytes (as *Erigeron pulchellus, Salvia lyrata*), and higher, occasional heaths (Oxydendrum, Vaccinium) emphasize the contrast with the north slopes. Outcropping sandstone layers near the top of the slope (area 6 of chart, Fig. 20) introduce local features.

[12] A few examples of tree sizes may be of interest: *Magnolia acuminata*, 55 ins., d.b.h.; *Aesculus octandra*, 47 ins., d.b.h.; *Fagus grandifolia*, 49 ins., d.b.h.; *Juglans nigra*, 36 ins., d.b.h.; *Sassafras variifolium*, 24 ins., d.b.h.

The contrast in the opposing slopes of Limestone Creek appears to be not entirely due to slope exposure. A resistant sandstone outcropping on the south slope (there is none on the Pine Mountain slope) locally increases the xerophytism and accounts for the occurrence of pines. With this exception, these southerly slopes are essentially like south slopes studied on Black Mountain (Braun 1940).

CUMBERLAND AND STONE MOUNTAINS

No major longitudinal valley skirts the inner base of Cumberland and Stone Mountains; in places there are valleys, but they are not continuous. The inward (northwest) slope of these mountains is much more irregular than is the inner slope of Pine Mountain and in many places there are short more or less parallel ridges between them and the interior area.

The Virginia slope of Cumberland Mountain is occupied by mixed mesophytic forest, but in general lacks the basswood that is so abundant in more typical parts of that forest. On lower hills along the base of the mountain, beech and white oak are abundant; in places, there is basswood. Actually, most of the forest cover is secondary, and only from evidence obtained in scattered stands is it possible to reconstruct something of the general forest type, which seems to accord well with the usual southerly slope aspects of the Cumberland Mountains.

FIG. 18. Tulip trees in the sugar maple-basswood-buckeye-tulip tree community of the northwest slope of Pine Mountain above Limestone Creek.

AREA NUMBER	V	IV	III	II	I	1	2	3	4	5
NUMBER of TREES	55	92	55	57	66	144	104	107	71	62
Fagus grandifolia										
Acer saccharum										
Liriodendron tulipifera										
Tilia heterophylla +										
Aesculus octandra										
Castanea dentata										
Magnolia acuminata										
Fraxinus americana										
Quercus montana										
Quercus alba										
Quercus borealis maxima										
Carya spp.										
Nyssa sylvatica										
Juglans cinerea										
Juglans nigra										
Cladrastis lutea										
Robinia pseudo-acacia										
Ulmus americana										
Magnolia tripetala										
Carpinus caroliniana										
Sassafras variifolium										
Morus rubra										
Acer rubrum										
Tsuga canadensis										

FIG. 19. Percentage composition of canopy of forest communities (at location 17 on map) on the northwest slope of Pine Mountain, and along Limestone Creek, a longitudinal stream at the foot of the mountain. The profiles of the mountain slope and of the stream (steepness exaggerated) suggest the confluence of communities I and 1 in the valley. Area 5, just over the divide from the head of Limestone Creek, is included to show differences in forest due to slope exposure. See also Figure 20.

The dip slope of Cumberland Mountain south of Cumberland Gap descends to the valley of Little Yellow Creek, now Fern Lake (location 18 on map). Although this is a northwesterly slope, the vegetation is remarkably similar to that of the southeast slope of Pine Mountain, with oaks and pines prominent in the canopy, and herbaceous and shrub layers made up of about the same species, although in places they appear to be more luxuriant. Where the dip slope faces almost north, the forest is prevailingly chestnut oak, with chestnut, hickory and tulip tree also abundant. The undergrowth is mesophytic. Ravines are similar to those of the dip slope of Pine Mountain with beech, hemlock, tulip tree, red maple, and white oak, and an undergrowth in which are *Cornus florida, Magnolia tripetala, Rhododendron maximum, Kalmia*

latifolia and a variety of deciduous shrubs. Ravine slope forests soon give way laterally to the prevailing oak-pine of the mountain slope. The structural and soil features appear to be more important in their control of vegetation than does slope exposure. All parts of Cumberland Mountain which have been seen are so modified by fire and cutting that no detailed studies were made.

Farther north, on Stone Mountain, the general vegetational features of Pine and Cumberland mountains are seen. Pines prevail wherever there is sandstone outcropping on dry slopes. When, inward, the strata become horizontal, the aspect at once changes, the whole becomes mixed mesophytic forest, for no longer are there shallow soil areas over dipping sandstone rocks.

THE OUTLYING AREA: MOUNTAINS EXTERIOR TO THE FAULT BLOCK

Beyond the limits of the fault block (that is, the highest and most characteristic part of the Cumber-

AREA NUMBER	1	2	3	4	5	6	7	8
NUMBER of TREES	82	44	117	37	42	34	56	26
Quercus coccinea								
Quercus montana								
Castanea dentata								
Nyssa sylvatica								
Liriodendron tulipifera								
Quercus borealis maxima								
Quercus alba								
Fagus grandifolia								
Tilia heterophylla								
Juglans nigra								
Carya spp.								
Acer saccharum								
Acer rubrum								
Fraxinus americana								
Magnolia acuminata								
Quercus velutina								
Robinia pseudo-acacia								
Pinus rigida								
Pinus echinata								
Cornus florida *								
Magnolia tripetala *								

FIG. 20. Percentage composition of canopy of forest communities on the south slope of Limestone Creek. See also Figure 19. *Cornus florida* and *Magnolia tripetala*, usually species of the understory, rarely approach a canopy position.

land Mountains), a large area to the west and south-west is sufficiently similar topographically and vegetationally to be included in the Cumberland Mountains. Mixed deciduous forest prevails throughout this outlying portion of the Cumberland Mountains, except where occasional outcrops of massive sandstone interrupt the otherwise even although steep slopes, or cap high ridges. In such places, pine generally mingles with oaks, although nowhere is it conspicuous as on Pine Mountain. Because of the lesser relief and lower summit altitudes in the outlying area than in most of the more typical parts of the Cumberland Mountains, none of the higher altitude features are seen; the sugar maple-basswood-buckeye-tulip tree community is poorly represented or absent; beech goes nearly to the tops of the ridges, hence is a constituent of most of the forest communities, except those of dry narrow ridge tops.

The mixed mesophytic forest is, then, more homogeneous (if a mixture may be thought of as homogeneous); that is, there is less regrouping of dominants and formation of association-segregates. Individual stands therefore more closely approach the abstract concept of mixed mesophytic forest. Variations in composition in relation to slope exposure are seen, most conspicuous of which is the white oak-beech of south slopes. However, these variations are not often distinct enough to recognize as distinct communities. Altitudinal variations do not complicate those induced by slope exposure.

The western part of the Cumberland Mountains in the vicinity of Williamsburg and east of Pine Knot is a maturely dissected area of strong relief, topographically distinct from the adjacent submaturely dissected Cumberland Plateau. This topographic difference accentuates a vegetational boundary that would otherwise be obscure. Mixed mesophytic forest with almost pure secondary groves of tulip trees on northeast slopes contrasts with the oak, oak-pine or beech woods of the flatter areas of the Plateau.

Northward, however, the Cumberland Plateau is more maturely dissected and rises gradually toward Pine Mountain, although everywhere with summit elevations lower than Pine Mountain. Here there is no other boundary than the structural one which is Pine Mountain. However, the forests of the higher dissected area near to Pine Mountain are distinctly of the Cumberland Mountains type, hence are included here. This will include the headwaters areas of the Kentucky River drainage southwest of Whitesburg, namely, the upper part of Leatherwood Creek, of Middle Fork, and of Red Bird River.

North and east of the northern terminus of Pine Mountain is a high strongly dissected part of the Plateau which extends east between the Cumberland Mountains and the Allegheny Mountains to the Ridge and Valley Province. There, the mixed mesophytic forest of the Cumberlands is continuous with that of the Plateau, and across it into the Allegheny Mountains of West Virginia. This area of dissected plateau is adjacent to and scarcely distinguishable from the northern end of the Cumberland Mountains in Virginia. This area in Virginia to the northeast of Flat Gap is in the drainage basin of Russell and Levisa Forks of the Big Sandy River. Much of it is very deeply dissected and rugged; the ridge-tops are very narrow, and the streams in places are in deep gorges. The whole area is occupied by mixed mesophytic forest. Within the range of the picture (Fig. 21) are:

Fagus grandifolia	*Magnolia acuminata*
Tilia heterophylla	*Nyssa sylvatica*
Tilia sp.	*Tsuga canadensis*
Acer saccharum	*Oxydendrum arboreum*
Liriodendron tulipifera	*Carya ovata*
Quercus borealis maxima	*Acer rubrum*
Aesculus octandra	*Quercus alba*
Castanea dentata	*Carpinus caroliniana*
Betula alleghaniensis	*Cornus florida*
Juglans nigra	*Magnolia tripetala*
Juglans cinerea	

Beech goes almost to the top, even on west slopes; in places on southerly slopes the crowns of beech and tulip tree project above the top of the ridge. White oak is more abundant on drier slopes.

Studies in three areas to the west of Pine Mountain are included: the forest of Lynn Fork of Leatherwood Creek, in Perry County (location 19 on map); of Nolans Branch of Red Bird River in Clay County (location 20); and of Buck Branch of Jellico Creek in Whitley County (location 21).[13]

LYNN FORK OF LEATHERWOOD CREEK

The forest of Lynn Fork of Leatherwood Creek was the most magnificent area of deciduous forest, surpassing anything else in the Cumberland Mountains or elsewhere which the writer has ever seen (Figs. 22-30 and Table 2). Here was "a forest of superlative beauty, forest of towering trunks, of luxuriant undergrowth, of exquisite ground cover."

Changes in slope exposure are reflected in changes in relative abundance of the constituent species of the canopy, yet everywhere except on the encircling ridges some phase of mixed mesophytic forest prevails (Fig. 23).

On southerly, southeasterly, and southwesterly slopes, white oak, beech, and in places tulip tree, are most abundant. White oak is here a tree with tall columnar trunks about four feet in diameter. In narrower parts of the valley, and in the vicinity of sandstone ledges, hemlock mingles with the deciduous species, but assumes a position of dominance only in a few places. The influence of the conifer leaf litter and of continuous shade is seen in the changed character of the lower layers of the forest. The mixed mesophytic forest with hemlock has the greatest density of any forest community in the area (Fig. 24).

[13] Lynn Fork of Leatherwood was logged soon after these studies were made and before some additional desirable data concerning white oak reported to be important on another slope were obtained; the forest of Nolans Branch has doubtless been cut as logging operations in upper Red Bird River were almost within hearing distance in 1935; the forest of Buck Branch was intact in the spring of 1939.

Locally, the ravines broaden into small areas known as "bottoms" (Fig. 29). These are not alluvial bottoms, merely nearly level areas. Toward the upper part of the right branch of the Left Fork of Lynn Fork, tulip tree increases in abundance and in size; trees average 14 feet in circumference. Beech and tulip tree (Fig. 25), and higher, sugar maple and tulip tree (Fig. 26) are the dominant species. The largest tulip tree known in or near the Cumberland Mountains grew here (Fig. 27). The undergrowth is exceedingly luxuriant, including a great variety of herbaceous plants and many large ferns (Fig. 26). The humus layer is deep mull.

On the highest slopes and ridges the more characteristic species of the mixed mesophytic forest are rare or absent. The forest is dominantly chestnut oak and chestnut, with an ericaceous undergrowth (Fig. 30).

Studies were made along the route shown on the accompanying map, Figure 22. These illustrate the great amount of variation in composition that is possible with little change in constituent species, except on the highest ridges, and the essential continuity of a mixed mesophytic forest throughout the drainage basin. The accompanying chart (Fig. 23) illustrates the variations in forest composition in the Left Fork of Lynn Fork. A brief characterization of areas distinguished follows:

1. Slope south to southeast; steep.
2. Slope south and less steep.
3. Valley narrower.
4. Low in narrow valley: slope strewn with sandstone blocks; much *Rhododendron maximum*.
5. South slope at fork of creek. A heavy sandstone layer locally affects ground vegetation; Galax and Epigaea abundant.
6. More open valley (Fig. 24); soil of south slope probably shallow because of heavy sandstone layer now beneath surface; trees of slope not so large.
7. South slope; much white oak reproduction in a small area of windfall.
8. Reflects slight influence of a sandstone horizon.
9. Lower ravine slope; soil dark, not sandy.
10. Rich mesophytic aspect (Fig. 25).
11-12. Slopes gentle to steep on sides of cove or valley head; deep mull; very luxuriant aspect, many large ferns (Figs. 26, 27).
13. Upper slopes of cove; less luxuriant aspect.
14. Near 5, and near fork of creek; sugar maple very conspicuous in understory (Fig. 28).

FIG. 21. View in the rugged and deeply dissected portion of the Cumberland Mountains in the Russell Fork drainage northeast of Norton, Va.

15. Higher on slightly convex southeast slope.

16. Slightly concave part of slope.

17. South-southeast slope, slightly convex; white oak appears to be replacing dead chestnut.

18. Lowest ravine slopes and "bottoms" (Fig. 29).

19. Westerly slope, reflected in greater abundance of white oak and beech. Red azalea (*R. cumberlandense*) in full bloom July 12.

20. Higher southwest slope, somewhat transitional to oak-chestnut forest.

21. A south-southwest sloping ridge (not apparent on topographic map); larger proportion of chestnut on less steep parts; Kalmia layer; soil sandy (Fig. 30).

22. Uppermost slopes and ridge-top, divide between Lynn Fork and Oldhouse Branch; shallow soil over slightly dipping sandstone; aspect of southeast slope of Pine Mountain.

The most striking single feature of the Lynn Fork forest is the high percentage of tulip tree in the area as a whole, and especially in the northeast-facing cove which is the head of the right branch of the Left Fork of the creek (Figs. 26, 27). Here the tulip trees tower above all other species, and sugar maple, which anywhere else would look large, forms a second layer in the forest. Beneath these are the usual smaller trees of the understory. Timber cruises show 27 percent of the trees of this drainage basin to be tulip tree, comprising an estimated 58 percent of the board-foot volume of lumber. This latter figure emphasizes the large size of these trees.

Beech is abundant in all communities except those at highest elevations (areas 13, 21 and 22 on chart, which are above 2,000 feet). On southerly slopes, the abundance of white oak, with beech, is evident (areas 2, 6, 7, 17 of chart, Fig. 23). On southwest

TABLE 2. Undergrowth of forest communities of Lynn Fork forest shown in Figure 23. Note that the herbaceous plants of areas 20, 21, and 22 are, with few exceptions, different from those of all other communities. The herbaceous layer is important in distinguishing oak-chestnut communities.

SMALL TREES AND SHRUBS	1	2	3	4	5	6	8	9	10	11	12	13	14	15	18	19	20	21	22
Amelanchier canadensis				x							x						x		x
Asimina triloba	x					x	x	x											
Benzoin aestivale					x		x	x		x									
Bignonia capreolata	x																		
Carpinus caroliniana	x								x	x	x		x						
Cercis canadensis	x		x																
Cornus alternifolia	x																		
Cornus florida	x		x				x	x	x		x	x		x					
Evonymus americanus	x	x													x	x			
Gaylussacia baccata																			x
Hamamelis virginiana	x		x		x								x						
Hydrangea arborescens			x				x	x	x		x								
Ilex opaca												x			x	x	x	x	x
Kalmia latifolia				x	x	x										x	x	x	x
Magnolia Fraseri	x				x		x				x								
Magnolia tripetala		x		x													x	x	x
Oxydendrum arboreum	x		x		x			x	x							x	x		
Pieris quinquefolia	x		x				x			x	x					x	x	x	
Pyrularia pubera	x		x										x	x		x	x	x	
Rhododendron cumberlandense					x												x		x
Rhododendron maximum		x	x	x	x											x	x	x	x
Rhododendron sp.					x														
Rhus Toxicodendron	x						x	x	x	x	x		x						
Rubus sp.		x																	
Smilax Bona-nox	x	x																	x
Smilax glauca																			x
Vaccinium sp.																			x
Vaccinium stamineum							x												x
Vaccinium vacillans					x	x											x	x	x
Viburnum acerifolium																			x
Vitis cordifolia	x									x	x	x							

GROUND HEATHS

Chimaphila maculata				x	x										x			x	
Epigaea repens					x														
Gaultheria procumbens					x														
Galax aphylla					x	x													

FERNS

Adiantum pedatum	x		x	x				x	x	x		x	x						
Aspidium Goldianum					x	x													
Aspidium marginale				x															
Aspidium noveboracense	x	x	x		x	x	x	x				x		x	x				
Aspidium spinulosum	x	x									x								
Asplenium acrostichoides				x					x	x									
Asplenium angustifolium	x	x						x	x	x	x								
Asplenium angustum	x	x				x	x	x		'									
Botrychium virginianum	x						x	x	x	x	x								
Osmunda cinnamomea					x	x	x		x				x						
Phegopteris hexagonoptera	x	x				x		x		x	x								
Polypodium virginianum	x								x										
Polystichum acrostichoides	x	x	x	x	x	x	x		x	x		x	x						
Pteris aquilina																			x

HERBS

Andropogon scoparius																			x
Diarrhena diandra										x	x								
Panicum sp.																			x
Clintonia umbellulata					x														
Disporum lanuginosum					x	x			x	x	x	x	x		x				
Disporum maculatum										x									
Medeola virginiana			x		x									x					
Smilacina racemosa			x																
Trillium erectum								x											
Trillium grandiflorum								x	x										
Uvularia grandiflora								x	x		x								
Uvularia perfoliata										x									
Dioscorea quaternata		x	x		x														
Hypoxis hirsuta					x											x			
Iris cristata					x														
Cypripedium acaule			x	x															
Cypripedium parviflorum var. pubescens						x			x	x									
Epipactis pubescens												x				x			
Liparis liliifolia	x																		
Microstylis unifolia					x														
Orchis spectabilis								x	x										
Laportea canadensis	x					x	x	x	x		x								
Pilea pumila	x						x	x											

	1	2	3	4	5	6	8	9	10	11	12	13	14	15	18	19	20	21	22
Aristolochia Serpentaria							x						x						
Asarum canadense	x									x	x		x						
Polygonum virginianum										x	x		x						
Silene virginica			x										x						
Stellaria pubera													x						
Anemone quinquefolia															x				
Anemonella thalictroides										x	x								
Cimicifuga racemosa									x	x		x	x						
Clematis viorna													x						
Clematis virginiana										x									
Hepatica acutiloba									x	x	x								
Ranunculus hispidus			x			x			x										
Ranunculus recurvatus	x									x									
Menispermum canadense										x									
Caulophyllum thalictroides									x	x		x	x						
Sanguinaria canadensis	x	x							x	x	x		x	x					
Astilbe biternata			x	x					x	x	x		x						
Tiarella cordifolia	x		x						x	x	x		x						
Aruncus sylvester	x								x	x	x		x						
Potentilla pumila				x	x														
Asplicarpa monoica	x	x	x			x		x		x	x		x						
Desmodium grandiflorum		x			x		x	x	x		x								
Desmodium laevigatum		x																	
Desmodium nudiflorum		x		x															
Desmodium pauciflorum											x								
Desmodium rotundifolium	x				x											x			
Lespedeza hirta																			x
Tephrosia virginiana																			x
Viola caroliniana	x	x		x		x		x								x			
Oxalis grandis	x																		
Geranium maculatum	x	x						x	x	x	x	x	x						
Impatiens pallida									x										
Hybanthus concolor									x										
Viola blanda	x			x	x			x	x		x		x						
Viola hastata													x						
Viola palmata										x									
Viola rostrata	x								x	x			x						
Viola rotundifolia			x	x										x					
Passiflora lutea	x									x									
Circaea lutetiana	x		x							x	x		x						
Aralia racemosa	x								x	x	x		x			x			
Panax quinquefolium													x						
Angelica villosa																			x
Cryptotaenia canadensis									x										
Osmorhiza longistylis									x	x	x								
Sanicula sp.									x				x						
Taenidia integerrima																			x
Thaspium aureum			x																
Monotropa uniflora												x			x			x	
Lysimachia quadrifolia		x						x										x	
Asclepias quadrifolia											x								
Phlox divaricata	x										x								
Hydrophyllum canadense											x								
Hydrophyllum virginianum											x								
Phacelia bipinnatifida										x	x								
Cynoglossum virginianum	x											x	x						
Lappula virginiana			x																
Collinsonia canadensis	x	x	x						x	x	x		x	x					
Monarda clinopodia			x																
Gerardia laevigata					x													x	x
Galium lanceolatum												x							
Houstonia tenuifolia																x			
Mitchella repens	x		x	x	x	x	x	x						x	x				
Trioateum angustifolium									x	x	x								
Campanula americana	x																		
Campanula divaricata																			x
Antennaria plantaginifolia	x																		
Aster cordifolius																			
Aster divaricatus		x									x								
Aster patens																			x
Coreopsis major							x												x
Erigeron pulchellus		x	x																
Eupatorium purpureum		x							x	x	x		x						
Eupatorium urticaefolium	x	x									x								
Hieracium paniculatum		x																	
Krigia amplexicaulis		x	x		x														
Polymnia uvedalia										x									
Prenanthes serpentaria																			x
Senecio obovatus	x	x																	
Sericocarpus asteroides	x		x																
Solidago caesia		x										x							
Solidago latifolia			x								x	x	x		x				

slopes (illustrated by area 20) beech comprises 17 percent of the oak-chestnut forest. In the deepest ravines, beech is associated with hemlock.

Chestnut is present in almost all communities, ranging from the most mesophytic hemlock-beech forest of deep ravines, to the dryest sandstone ridge-tops, where associated with chestnut oak and pine. As in the Black Mountain area (Braun 1940) its presence, even in abundance, can not be taken as an indication of oak-chestnut forest. The lower layers of the forest (shrub and herb) and the nature of the soil and humus layer will distinguish the oak-chestnut communities (Fig. 30 and areas 20, 21, 22 of chart, Fig. 23). Chestnut is, of course, nearly dead as a

result of blight. What will take its place in the future forest must be determined for each community separately. Usually it is one of the less tolerant species of the community: chestnut oak (*Quercus montana*) in the oak-chestnut areas; white oak in communities in which this species is well represented (as 17 of chart); sugar maple in the more meso-phytic communities.

The undergrowth of the Lynn Fork forest varied from place to place, both in luxuriance and in composition (see Table 2). The species of the last three communities (20, 21, 22 of Fig. 23 and Table 2), which comprise the oak-chestnut forest of the area (Fig. 30), are almost all different from those of the
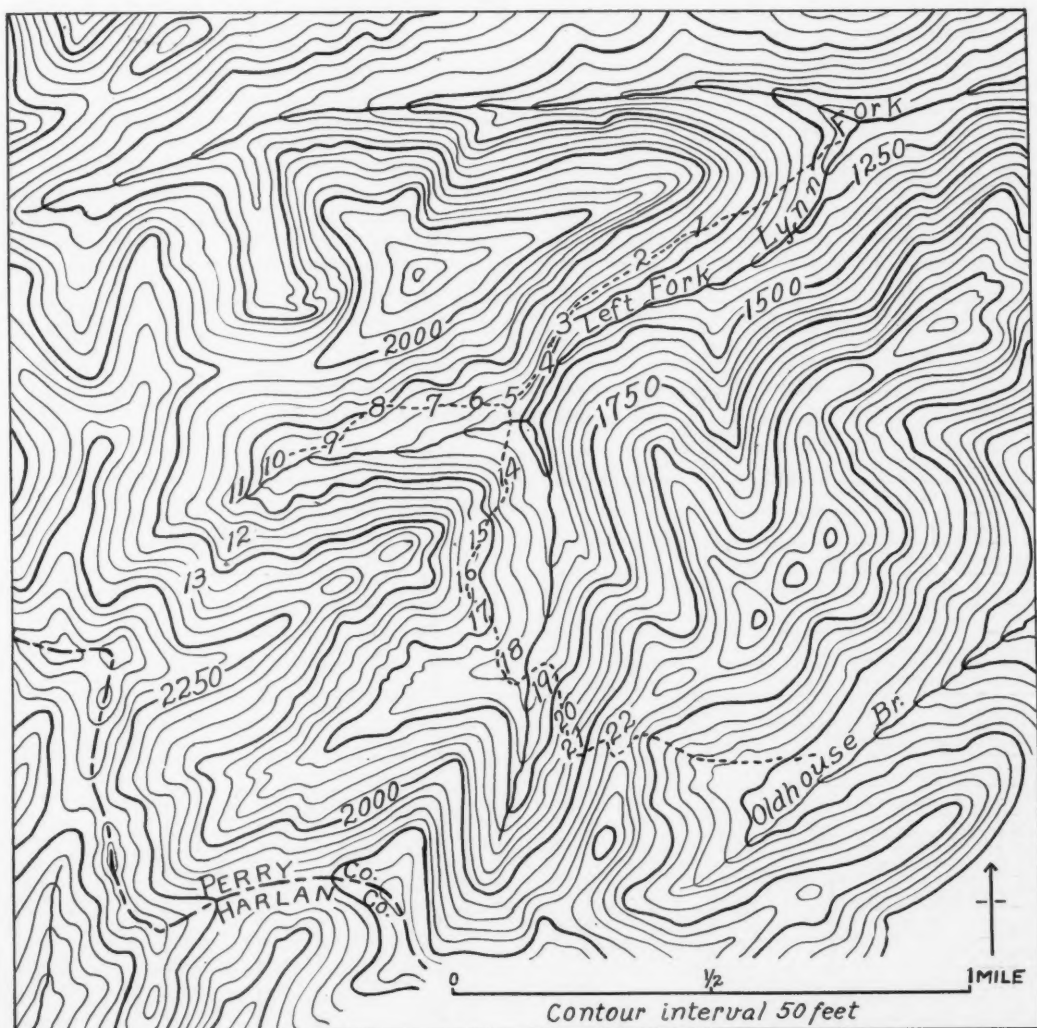
FIG. 22. Topographic map of the drainage basin of Lynn Fork of Leatherwood Creek (location 19 on map, Fig. 1). Numbers give location of forest communities distinguished on chart, Figure 23. Adapted from Cornetts-ville topographic sheet.

remainder of the forest. Sandy soil (where sand-stone substratum is not far below surface) affects to a slight extent the undergrowth of a few communities (for example, 4, 5, 6, 8). The richest undergrowth and the deepest mull is in the tulip tree-sugar maple forest of the right branch of the creek (areas 11, 12), illustrated in Figures 26 and 27. The beech-tulip tree area (area 10 and Fig. 25) is almost as rich.

NOLANS BRANCH OF RED BIRD RIVER

Areas studied on Nolans Branch were less con-tinuous than those in Lynn Fork. The series selected represents differences in slope exposure, with little altitudinal range (see chart, Fig. 31). Regardless of exposure, mixed mesophytic forest prevails. There is no massive rock in the area, hence all slopes are about equally reduced, and nowhere exceedingly steep. One small area on a northerly slope approaches the sugar maple-basswood-buckeye-tulip tree type of the higher Cumberlands. Elsewhere, beech is present, although variable in amount. Every community is mixed, and even on southwesterly slopes where chest-nut oak is abundant, all of the more characteristic mesophytic species except buckeye are present.

BUCK BRANCH OF JELLICO CREEK

Buck Branch of Jellico Creek is an eastward-flow-ing stream only a few miles from the western border

of the Cumberland Mountains east of Pine Knot (location 21 on map, Fig. 1). Although the low vegetation has been somewhat affected by hogs and sheep, most of the species are probably represented in sheltered or inaccessible spots. The tops of large sandstone blocks lying on lower slopes (derived from higher strata which form the ridge crests) are veri-table flower gardens with *Sedum ternatum, Arisaema triphyllum, Smilacina racemosa, Trillium Hugeri*, plants which should be abundant throughout the ground layer. In respect to canopy, the forest is a virgin stand affording opportunity for study of ravine and slope forests of different exposures. The similarity of the ravine and north slope forests is apparent (Fig. 33). The topographic locations of areas distinguished on the chart are shown in Figure 32. On the lower south slopes, the beech-white oak or beech-white oak-tulip tree forest type prevails, giving way upward to oak-tulip tree and finally, on the rocky very steep uppermost slopes, to chestnut oak forest with an open heath layer and sparse sandy soil herbaceous flora. On these highest slopes the rocky immature soil is covered by a thin layer of mor. Elsewhere the mull humus layer of the mixed forest prevails. These differences are reflected in the composition of lower layers (Table 3). Farther downstream (and below this area of uncut forest)

AREA NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	T exc 20.22	%	T 20.22	%
NUMBER OF TREES	110	35	81	55	74	73	39	17	46	46	81	31	36	58	45	91	39	50	18	30	74	49	1025		153	
Fagus grandifolia																							268	26.2	5	3.3
Liriodendron tulipifera																							184	18.0	1	.6
Tsuga canadensis																							108	10.5		
Quercus alba																							105	10.3	7	4.6
Acer saccharum																							84	8.2		
Castanea dentata																							60	5.8	41	26.8
Acer rubrum																							43	4.2	9	5.9
Betula alleghaniensis																							36	3.5		
Tilia heterophylla																							33	3.2		
Nyssa sylvatica																							28	2.7	2	1.3
Quercus borealis maxima																							20	2.0		
Carya spp.																							19	1.8	1	.6
Magnolia acuminata																							11	1.1		
Juglans nigra																							9	.9		
Magnolia Fraseri																							7	.7		
Aesculus octandra																							3	.3		
Quercus montana																							3	.3	59	38.6
Fraxinus americana																							2	.2		
Juglans cinerea																							1	.1		
Pinus rigida																									17	11.0
Pinus echinata																									5	3.3
Quercus coccinea																									6	4.0

FIG. 23. Percentage composition of canopy of forest communities in Lynn Fork of Leatherwood Creek (loca-tion 19 on map, Fig. 1). See also Figure 22 and Table 2.

hemlock occurs locally on low sandstone cliffs near the stream level.

BEYOND THE LIMITS OF THE CUMBERLAND MOUNTAINS

In order to contrast the forests of the Cumberland Mountains with those on the adjacent maturely dissected plateau, Figure 34 is included. Beyond the limits of the Cumberland Mountains (at location 22 on map, Fig. 1), forest composition on various slope exposures, in ravines, and on ridges was determined. This area is representative of a considerable part of the maturely dissected plateau of low relief, about 500 to 700 feet; it is neither representative of the more deeply dissected parts nor of the dissected margin of the plateau, in both of which areas there are typical mixed mesophytic forests.

Local variations occur on the several slope exposures, due to irregularities in steepness and to slight differences of slope exposure introduced by convexities and concavities of slope. Beech extends about half way up south and west slopes and two thirds or more of the way up east and north slopes. Tilia is prominent on north and east slopes, absent from south and west slopes. Ridges vary as to dominance of chestnut oak or scarlet oak; nowhere is chestnut a dominant in the ridge forest. As compared with the Cumberland Mountains, there is a striking increase in the dominance of beech and of white oak, and an equally striking decrease in the proportion of other dominants of the mixed mesophytic forest—basswood, buckeye, sugar maple, tulip tree, red oak—yet all are present, and in actual number of tree species this forest compares favorably with

TABLE 3. Undergrowth of forest communities of Buck Branch forest shown in Figure 33.

UNDERSTORY TREES, CANOPY SPECIES	N3	N2	N1	R1	R2	R3	R4	S1	S2	S3	K
Fagus grandifolia		x	x	x	x	x		x	x	x	
Acer saccharus	x	x	x	x	x	x	x	x	x	x	x
Aesculus octandra	x		x	x	x		x				
Tilia heterophylla	x	x				x	x				
Castanea dentata							x				
Liriodendron tulipifera		x		x			x	x			
Quercus montana								x	x	x	
Quercus alba	x						x	x	x		
Carya alba		x						x			
Carya cordiformis		x	x								
Carya glabra							x	x			
Carya ovata						x	x	x			
Quercus borealis maxima		x			x		x	x			
Fraxinus americana		x	x	x		x	x	x	x		
Nyssa sylvatica			x				x	x	x		
Quercus velutina							x	x			
Magnolia acuminata		x			x						
Acer rubrum			x				x	x	x	x	
Juglans nigra	x	x	x								
Cladrastis lutea	x	x	x			x					
Juglans cinerea			x								
Ulmus alata				x							
Liquidambar styraciflua			x								
Robinia Pseudo-Acacia								x			
SMALL TREES AND SHRUBS											
Amelanchier canadensis								x			x
Asimina triloba	x	x	x	x	x	x		x	x		
Benzoin aestivale			x	x							
Carpinus caroliniana		x	x	x	x	x		x			
Cercis canadensis	x									x	
Cornus florida	x	x	x	x	x	x	x	x	x	x	x
Crataegus sp.			x								
Gaylussacia baccata											x
Hydrangea arborescens			x	x							
Oxydendrum arboreum								x	x	x	x
Psedera quinquefolia	x					x		x	x		
Rhododendron cumberlandense								x		x	
Rhus Toxicodendron	x							x	x		
Smilax glauca									x		
Smilax Bona-nox								x	x		
Vaccinium arboreum										x	
Vaccinium simulatum								x	x		
Vaccinium stamineum									x		x
Vaccinium vacillans								x		x	x
FERNS											
Adiantum pedatum		x	x	x	x		x	x			
Aspidium noveboracense			x				x				
Asplenium acrostichoides			x	x	x						
Asplenium angustifolium			x								
Asplenium angustus									x		
Asplenium platyneuron									x		
Botrychium virginianum		x							x		
Camptosorus rhizophyllus						x					
Phegopteris hexagonoptera		x	x	x	x		x				
Polypodium virginianum										x	
Polystichum acrostichoides			x	x	x			x	x	x	

HERBS	N3	N2	N1	R1	R2	R3	R4	S1	S2	S3	K
Festuca octoflora											x
Poa cuspidata											x
Arisaema triphyllum	x		x	x	x	x	x				
Luzula sp.									x		
Disporum lanuginosum		x									
Erythronium americanum	x	x	x	x	x	x	x				
Medeola virginiana								x			
Polygonatum biflorum		x	x								
Smilacina racemosa				x	x	x	x	x			
Trillium erectum		x	x			x					
Trillium grandiflorum						x	x				
Trillium Hugeri	x	x					x	x			
Uvularia perfoliata								x			
Dioscorea sp.		x	x								
Iris cristata				x	x			x			
Aplectrum hyemale	x										
Tipularia discolor								x			
Laportea canadensis			x			x					
Asarum arifolium								x			
Stellaria pubera		x						x			
Claytonia caroliniana	x	x	x	x							
Claytonia virginica											x
Anemone quinquefolia		x									
Anemonella thalictroides	x	x	x		x	x	x	x	x		x
Cimicifuga americana	x										
Cimicifuga racemosa	x	x	x	x	x	x					
Hepatica acutiloba				x	x	x	x				
Ranunculus hispidus				x	x		x				
Ranunculus recurvatus			x	x							
Caulophyllum thalictroides		x	x	x	x	x	x				
Podophyllum peltatum			x	x	x	x	x				
Sanguinaria canadensis	x	x	x								
Cardamine parviflora									x		
Dentaria diphylla		x									
Dentaria heterophylla	x	x	x	x	x	x	x				
Dentaria laciniata			x	x	x	x					
Sedum ternatum	x		x			x	x				x
Heuchera americana	x								x		x
Tiarella cordifolia			x	x	x						
Potentilla canadensis									x		
Potentilla pumila										x	
Desmodium rotundifolium									x		
Lespedeza spp.									x		
Vicia caroliniana								x	x	x	
Oxalis violacea			x					x	x	x	
Geranium maculatum								x	x		
Impatiens pallida			x								
Ascyrum hypericoides									x		
Viola hirsutula								x			
Viola papilionacea		x									
Viola scabriuscula				x	x						
Panax quinquefolium	x		x								
Panax trifolium		x									
Erigenia bulbosa			x	x	x	x	x				
Chimaphila maculata		x									
Phlox divaricata		x		x	x	x	x				
Cynoglossum virginianum		x					x				
Myosotis macrosperma											x
Cunila origanoides								x	x		
Conopholis americana		x									
Houstonia caerulea			x				x	x	x		
Antennaria plantaginifolia								x	x		
Coreopsis major								x	x		
Eupatorium urticaefolium	x	x		x	x	x	x	x			
Hieracium venosum								x	x		
Krigia virginica									x		
Solidago caesia								x			

forests in the Cumberland Mountains. Here also, chestnut is much less abundant, and Carya (all species taken together) is much more abundant than in the Cumberland Mountains.

The topography, and the poorer soil, appear to be related to stratigraphic horizon, and thick shale beds. As a result, a poorer type of mixed mesophytic forest has developed, a forest not referable, however, to any other major association. Because of slower water penetration into the shales and subsoils derived from them, erosion of humus is more rapid after clearing than it is on more porous soils. Secondary forests in such areas are prevailingly oak-hickory. It may be features of this sort which have influenced some to map the plateau as "oak-hickory" (Kendeigh 1934). Only on a few ridge crests is there any primary oak-hickory. There it occupies the same situations as does oak-chestnut and is its ecological equivalent; both are physiographic climaxes in the area of the mixed mesophytic association.

FOREST COMMUNITIES OF LARGER VALLEYS

Although the emphasis in the present paper is upon climax and physiographic climax forest communities, consideration of seral stages of river valleys is of importance, both because there are features here not common to the whole deciduous forest, or even to the whole area of the mixed mesophytic climax, and because successional development demonstrates the establishment of a mixed mesophytic forest on valley floors essentially like that of mountain slopes.

THE VALLEY FLOORS

Few areas of natural vegetation remain on valley floors. There is so little land suitable for cultivation in the Cumberland Mountains, that almost every acre of relatively level land is utilized, unless it is adjacent to streams and subject to frequent overflow, or is swampy or poorly drained. Seral vegetational stages occupy such places. A few very small areas of forested mesic valley flats along small streams have been seen; these always support mixed mesophytic forest. In larger valleys scattered trees or groups of trees left along roads may be used as evidence from which to reconstruct the mesophytic forest types of valley floors.

Stream Margins

In many places, mountain slopes descend directly to stream margins; slope forest with no admixture of river border trees may continue to within a few feet of the stream (Fig. 35). Depositing shores, even if narrow, usually have a fringe of trees of

FIG. 24.   Looking south from area 6 of map, Figure 22, in the Lynn Fork forest.   Hemlock, birch, tulip tree, white oak, beech and sugar maple are abundant in this part of the forest.   June 14, 1933.

species not general elsewhere. The widely distributed streamside trees—sycamore, black willow, box elder, white elm and silver maple—are of course present, although not all are to be expected in any one area. River birch *(Betula nigra)* is conspicuous and in many places is the most abundant tree (Fig. 35). Sweet gum *(Liquidambar styraciflua)* is sometimes abundant. *Ulmus serotina* may be present. In places, more or less extensive sycamore flats are seen; sweet gum is usually mingled with the sycamore, and *Magnolia tripetala* may be abundant as an understory tree—flats of Red Bird River below Beverly (Fig. 36). Bamboo *(Arundinaria macrosperma)* is sometimes abundant.

Immediately back of the margin, an admixture of mesophytic species indicates the early replacement of marginal species when habitat conditions permit. In fact, the forest of mesic valley flats may in places have no border of marginal species. If depositing areas are small (and hence shaded by adjacent forest) and variation in stream height little, or periods of overflow of very short duration, as is true of some smaller streams, trees of the climax forest may pioneer in the bare areas of deposition. Young hemlock,

beech, tulip tree, red and sugar maple, together with sycamore initiate a new community on the depositing shore.

Swampy or Poorly Drained Flats

West of Pine Mountain and near to the Cumberland River, wide valley flats extend into the mountains from the Cumberland Plateau like narrow tongues. Little of the original forest remains; the scattered trees indicate former occupancy by swamp forest in which sweet gum, willow oak *(Quercus phellos)*, swamp white oak *(Quercus bicolor)*, winged elm *(Ulmus alata)* and red maple were important species. On slightly higher flats, southern red oak *(Quercus falcata)* is common, generally associated with sweet gum and sometimes with beech. Swamp meadows and alder thickets (secondary vegetation) are of frequent occurrence.

Within the Cumberland Valley above Pine Gap, swamps are small and local, confined to cut-offs and seepage areas near the base of mountain slopes. Somewhat larger swamps occur in the valley of Clear Creek. Although adding to the diversity of vegetation and increasing the flora of these mountains, such areas are ecologically unimportant.

Fig. 25. Beech and tulip trees prevail in area 10 (map, Fig. 22). The figure beside tulip tree in center of picture gives some impression of relative sizes. The herbaceous layer and low woody layer are very luxuriant. June 14, 1933.

FIG. 26.   In a grove of giant tulip trees (area 11); ferns, *Asplenium angusti-folium*, are conspicuous in the luxuriant ground cover.   June 14, 1933.   Courtesy Nature Magazine.

Mesic Valley Flats

Small areas of low alluvial or sandy terraces border the Cumberland River and some of its tributaries above Pine Gap. On a few of the smallest of such areas, secondary forests have developed; elsewhere the land is utilized and only scattered trees along roads remain as evidence of the former mixed meso-phytic forest, which contained beech, tulip tree, white oak, chestnut, walnut, butternut, basswood, red maple,

sweet birch, hemlock, and doubtless other species. It is said that in some places rhododendron formed impenetrable thickets in this forest. The low slopes leading to such terraces were occupied by mixed forest.

Young secondary forest on small terrace remnants (in the upper Cumberland Valley and along Clear Creek) contains, in addition to a number of the meso-phytic tree species mentioned above, *Cornus florida*,

Magnolia tripetala, M. macrophylla, Nyssa sylvatica, Diospyros virginiana, Aralia spinosa, Cercis canadensis, Ilex opaca, Clethra acuminata, Stewartia pentagyna, Hamamelis virginiana, etc. In places where the soil is very sandy, pines *(Pinus rigida, P. virginiana)* sometimes form dense groves.

LOW HILLS OF THE MIDDLESBORO BASIN

Areally unimportant, but ecologically interesting, are the low hills in the Middlesboro basin. As most of these are occupied by the outskirts of the city of Middlesboro, only fragmentary evidence remains concerning their forest cover. Oaks prevail; the soil is the yellow-red prevalent southward. The combination suggests an outlier here of the oak forest type of the red and yellowerths, the zonal soil type to the south of the area of the mixed mesophytic forest.

DISCUSSION

The Cumberland Mountains are the center of distribution of the mixed mesophytic association of the deciduous forest (Braun 1941). Here variations in composition of the mixed forest due to shifting dominance or changing numerical importance of species give rise to association-segregates, some of which help to demonstrate the relationships and mode of origin

FIG. 27. Tulip tree (area 12), 23 feet in circumference 4 feet above the up-slope side of the base. Ferns and *Aralia racemosa* in foreground. June 14, 1933.

of the great climax units of the deciduous forest. Large size attained by individuals, large number of species comprising the forest, and wide range of habitat occupied by many of the climax species further demonstrate that here is the optimum area for mixed mesophytic forest.

Large size of individuals—a feature of a center of distribution—is apparent from figures of diameters and photographs in this and preceding papers. *Aesculus octandra* (Fig. 17) frequently exceeds the size range of this species given by Sargent (1933), as do also *Magnolia acuminata, Castanea dentata* (straight columnar form), *Quercus borealis* var. *maxima* and others. Tulip tree reaches enormous size (Fig. 27). Sugar maple (Fig. 8) is larger than in the Great Smokies.

The number of species of the forest canopy, often twenty or over, is a feature of the mixed mesophytic forest, a feature strikingly emphasized in October during the period of fall coloration, and evident on all the charts of percentage composition.

The wide range of habitats occupied by climax species in the forests of the Cumberland Mountains is readily ascertained from charts of forest composition in this and previous papers (Braun 1935, 1940). Most conspicuous in this respect is beech. Frequent repetition has been made of the presence of beech in south slope communities and of its higher altitudinal range on warm (south or west) slopes. In addition, beech is a constituent of ravine forests and of many ridge crest communities. Beech in the Cumberland Mountains, the center and optimum area of the mixed mesophytic forest, has a wide habitat range. This is in contrast to the narrower habitat range of this species toward the geographic limits of the mixed mesophytic association (especially in the ecotone between the mixed mesophytic and oak-hickory climaxes). There it is often confined to the most favorable sites. For example, in western Kentucky where oak-hickory forest prevails, beech occurs on the more mesophytic ravine slopes and in gorges where may be seen outliers (relies) of the mixed mesophytic forest. In the Knobs region of Indiana, beech is more generally confined to northerly slopes, while oak-hickory forest occupies the southerly slopes (Potzger & Friesner 1940).

As was pointed out in the Black Mountain area (Braun 1940), chestnut has an exceedingly wide community range. It is present in almost every community in the Cumberlands (see percentage lists and charts) from the drier ridge crests to the most mesophytic ravine communities with hemlock, and on alluvial flats.

The position of tulip tree in the climax mixed mesophytic association of the deciduous forest may be questioned, just as is that of white pine in the northern hardwood or Lake forest (Nichols 1935, Graham 1941). Tulip tree is an abundant species in certain communities, especially in some areas of the sugar maple-basswood-buckeye association-segregate. It occurs commonly in deep ravines with hem-

FIG. 28. Beech, tulip tree, and sugar maple (in area 14); sugar maple is very abundant in the understory. July 12, 1935.

FIG. 29. Small more or less flat areas such as this (area 18) are often referred to as "bottoms." Ferns *(Aspidium noveboracense)* and Kalmia beneath the beech, hemlock, and sugar maple. July 12, 1935.

FIG. 30. Chestnut oak-chestnut forest of a south-southwest sloping ridge (area 21) with a small tree layer in which dogwood is a subdominant, and a shrub layer of Kalmia. July 12, 1935.

lock and beech; it is one of the dominants in the chestnut-sugar maple-tulip tree association-segregate. In fact, it is present in most communities but less abundant in the more xeric ones. Apparent tolerance is influenced by favorable habitat factors (Toumey & Korstian 1937). Although generally considered as an intolerant tree, Liriodendron in the Cumberland Mountains reacts to the optimum conditions of this area, thus displaying an apparent tolerance which may largely account for its presence in a wide variety of communities. It may thrive in the open, as demonstrated by the many small secondary stands of this species. These, however, generally occupy sheltered situations—lower ravine slopes or coves on northerly mountain slopes. These cove forests of secondary tulip tree are a conspicuous feature of the Cumberland Mountains. Or, it may reproduce in the shade and in competition with other constituents of the mixed mesophytic forest. In almost every community studied in which it is a constituent of the canopy, thriving young individuals are seen, just as are young sugar maple, beech, and chestnut.

In a few areas of primary forest where Liriodendron is especially abundant, this abundance may be due to accident centuries ago. The secondary cove forests of today, two or three centuries hence, might resemble certain local areas seen in forests of north-

erly slopes. One such place was seen on Pine Mountain near the head of Limestone Creek (not included in chart). In one area in Lynn Fork where especially abundant, beech and sugar maple (large), together with other species of the mixed forest, might be considered as forming a layer below the canopy of Liriodendron. In such places, it might be considered as a remnant of a seral stage following, for instance, a tornado of the past. However, the general occur-

DIRECTION OF SLOPE	N-NE	N	NW	W-SW	ALL
NUMBER OF TREES	132	39	87	116	374
Fagus grandifolia					22.7
Liriodendron tulipifera					14.7
Castanea dentata					12.8
Quercus montana					10.2
Acer saccharum					9.6
Tilia heterophylla					5.4
Aesculus octandra					5.4
Quercus alba					3.8
Nyssa sylvatica					3.2
Magnolia acuminata					2.9
Betula alleghaniensis					2.9
Carya spp.					2.1
Acer rubrum					1.3
Quercus borealis maxima					.8
Juglans nigra					.5
Robinia pseudo-ocacia					.5
Juglans cinerea					.3
Fraxinus americana					.3
Quercus velutina					.3
Oxydendrum arboreum					.3

FIG. 31. Percentage composition of forest communities in Nolans Branch of Red Bird River (location 20 on map).
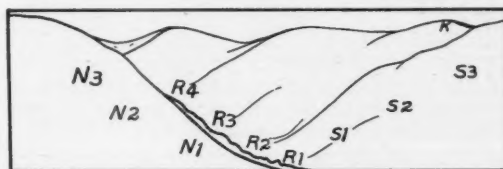
FIG. 32. Sketch designed to show topographic locations, in Buck Branch forest, of areas distinguished in chart, Figure 33.

rence of Liriodendron cannot be explained on a basis of past catastrophe. Neither does it appear that local windfalls, or the dying of canopy species, are necessary for the species to assume a canopy position. It would be difficult to account for its abundance and wide community range by accident alone. In most places, it appears to be as much a true constituent of the climax as do any other of the dominant species.

The most characteristic species of the mixed meso-phytic forest appear to be *Tilia heterophylla*[14] and

[14] Unfortunately, the taxonomic status of forms of Tilia in the mountains seems open to question. *T. heterophylla* is used here in a broad sense, and may include other species (as *T. Michauxii*) with leaves whitened beneath. Still other species of Tilia, with leaves green beneath, also occur. Because of height of trees and inaccessibility of flowering and fruiting branches, no attempt has been made to separate the species or varieties in the determination of percentage composition. The most abundant form is, however, the one with leaves whitened beneath, which appears to be typical *T. heterophylla*.

AREA NUMBER	N3	N2	N1	R1	R2	R3	R4	S1	S2	S3	K		T,N	T,R	T,S
NUMBER OF TREES	45	49	47	64	71	34	71	58	77	58	29		141	240	193
Fagus grandifolia													21.3	37.9	15.0
Acer saccharum													29.8	20.8	.5
Aesculus octandra													9.9	5.8	
Tilia heterophylla+													9.9	7.1	.5
Castanea dentata													3.5	3.8	1.5
Liriodendron tulipifera													3.6	3.8	14.5
Quercus montana													.7	4	22.8
Quercus alba													.7	4	20.2
Carya spp													4.3	2.5	7.8
Carya ovata													6.4	2.1	1.5
Quercus borealis maxima													5.0	2.1	2.6
Fraxinus americana+													.7	2.9	1.0
Nyssa sylvatica														.4	5.7
Quercus velutina															3.1
Magnolia acuminata													.7	2.1	.5
Acer rubrum															1.5
Juglans nigra													2.1	1.2	
Cladrastis lutea														2.9	
Juglans cinerea													.7	.4	
Ulmus americana													.7	.8	
Ulmus alata														.4	.5
Liquidambar styraciflua														2.1	
Robinia pseudo-acacia															.5

FIG. 33. Percentage composition of canopy of forest communities on Buck Branch of Jellico Creek (location 21 on map). North slope, south slope, and ravine forests distinguished by N, S, and R, respectively; K, knobs. See Figure 32 for topographic locations of communities.

SLOPE	Ra	N	S	E	W	Ri
NUMBER OF TREES	198	82	126	75	104	207
Fagus grandifolia						
Quercus alba						
Quercus montana						
Castanea dentata						
Quercus velutina						
Acer saccharum						
Carya glabra						
Carya sp.						
Tilia heterophylla						
Quercus coccinea						
Liriodendron tulipifera						
Carya ovata						
Nyssa sylvatica						
Quercus borealis maxima						
Juglans cinerea						
Carya cordiformis						
Magnolia acuminata						
Acer rubrum						
Aesculus octandra						
Fraxinus americana						
Oxydendrum arboreum						
Juglans nigra						
Ulmus americana						
Carya alba						
Betula lenta						
Sassafras variifolium						

FIG. 34. Percentage composition of canopy of forest communities of different slope exposures, of ravines, and of ridges near Peabody on Red Bird River (location 22 on map).

Aesculus octandra, although either or both may drop out before the geographical limits of this association are reached. Both are numerically important constituents of the mixed mesophytic forest of the Cumberland Mountains. Neither is a constituent of any other than mixed mesophytic forest. That the ranges of these species coincide fairly well with the limits of the mixed mesophytic forest is emphasized by a consideration of the limits of their ranges. Neither is listed by Fosberg and Walker (1941) for the Shenandoah National Park, which is east of the area of

dominance of the mixed mesophytic climax. Northward, their ranges terminate about where the mixed mesophytic forest ends (see Schaffner 1932, and map of distribution in Indiana, Deam 1940). Westward, these species drop out in the broad ecotone between the mixed mesophytic and the oak-hickory forests.

Climate alone is not sufficient to account for the dominance of this climax in this area. Past physiographic history, and the influence of the major soil type or zonal soil type (a reflection of climate) must also be considered.

A climate characterized by abundant and well-distributed precipitation and great temperature range with cold winters and hot humid summers marks this area (see Fig. 2). Westward the tendency to summer droughts is greater; southward the winters are more open. Dry summers are detrimental to the most mesophytic species. *Aesculus octandra* is the first of these species to be affected by deficient water; leaf-fall (due to dryness) may occur in July. Obviously, where summer drought is the rule, such a species would be eliminated because of shortness of the vegetative season. Open winters favor leaching of the soil, reducing its fertility. This is reflected in the development of the red-and-yellowerths, less favorable to mixed mesophytic forest, and generally

FIG. 35. Poor Fork of Cumberland River above Cumberland. Steep forested slopes of Black Mountain descend to river on the right. On the left, river birch *(Betula nigra)* overhangs the stream.

occupied by some type of oak or oak-pine forest. The development of the mull type of humus layer is inhibited on leached and acid soils. These soil factors, dependent on climate and affected by forest type, are in turn influential in maintaining the mixed mesophytic forest.

Wherever, within the area of the Cumberland Mountains, the optimum area of mixed mesophytic forest, the influence of underlying rock is so strong as to overcome the regional forces (as on dipping sandstone strata of Pine Mountain, and locally on sandstone ridges) the mixed mesophytic forest is interrupted. Some other forest type, generally oak-chestnut or pine, develops, maintaining itself as a physiographic climax on such dry slopes and ridges. Poorer soils, derived from some of the non-calcareous shales of the Pottsville series, sometimes result in an increase in the proportion of beech, if habitat factors are otherwise favorable to the development of the mixed mesophytic forest. The limits of the Cumberland Mountains vegetation are perhaps accentuated in places because of this. As an example, note the composition of forest communities near Peabody (at location 22 on map) a few miles up Red Bird River from Big Creek and some twenty-five miles down-

FIG. 36. Red Bird River near Nolans Branch. Mesophytic forest comes almost to the water's edge on the slope in the center of the picture. Sycamore on either side on flatter shores.

stream from its source, and 15 to 20 miles downstream from Nolans Branch (location 20).

Throughout the Cumberland Mountains, the dominance of mixed deciduous forest is evident. From any eminence from which one may view a thousand feet or so of mountain slope with its ravines and ridges, it is the impression of mixed forest which prevails. Some localization of species will appear here and there, but only near the ridge crests does any great change in forest take place. It is only closer observation within the forest that discloses the niceties of variation in composition and makes possible a correlation of these variations with habitat fluctuations. The recognition of association-segregates became a necessity in interpreting the forest as a whole (Braun 1935a). Unless all are recognized as integral parts of the climax, an interpretation of some of them as seral stages would be necessary. There is no evidence for this. If an hypothetical climax is conceived, which approaches in composition some one of the communities actually present, which shall be selected? And if microclimates resulting from the great diversity of topography are to be set aside in picturing a "regional" climate, what shall that climate be? The climate of the peneplain which may presumably some day occupy this location cannot be the climate of a mountainous area. The climate of the area together with the innumerable temperature and moisture variations—the microclimates—is a climate largely affected by the mountains which influence summer rains. The mixed mesophytic forest with its several association-segregates is the response to these conditions. Its areal distribution has been affected in the past by physiographic changes and accompanying climatic changes. It finds, in an area of mature topography resulting from the dissection of the ancient Cumberland peneplain (mid-Tertiary), and unaffected by later peneplains (as was the Ridge and Valley Province) an optimum area where is preserved a mixed forest enriched through the ages by migrations into it, and little affected by the profound changes which affected deciduous forest farther west and farther north.

SUMMARY

The area studied comprises the Cumberland Mountains physiographic section located in southeastern Kentucky and adjacent Virginia and extending into Tennessee; an area of approximately 5,000 square miles. The range of elevation is from about 1,000 feet to 4,250 feet. Subdivisions recognized in the area include (1) the higher and most characteristic central part, Black and Log Mountains; (2) the bordering monoclinal mountains with dipping strata, Pine, Cumberland and Stone Mountains; (3) a large section exterior to the fault block. The vegetation of these subdivisions is discussed separately.

Mixed deciduous forest of superlative quality originally covered most of the area. This is now represented by rapidly diminishing areas of virgin forest

and extensive cut-over and secondary stands. The emphasis throughout this paper is on original forest.

Studies show that forest composition varies with slope exposure and to some extent with altitude. Except in a few habitats, mixed mesophytic forest prevails. The variations in composition and shifting dominance of species of the mixed mesophytic forest are illustrated by charts showing percentage composition of canopy trees. The nature of the undergrowth correlates well with the composition of canopy. In all areas of mixed mesophytic forest, the mull type of humus layer has developed. Locally, departure from mixed mesophytic forest, due to extreme edaphic factors, is seen.

The Cumberland Mountains are the center of distribution of the mixed mesophytic forest. This is emphasized by the large number of association-segregates of the mixed mesophytic association, the large size of trees, large number of species in the canopy, and wide range of habitat of climax species.

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THE GROWTH AND DEVELOPMENT OF THE ROOT SYSTEMS OF JUVENILE LODGEPOLE PINE[1]

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THE GROWTH AND DEVELOPMENT OF THE ROOT SYSTEMS OF JUVENILE LODGEPOLE PINE

INTRODUCTION

The root systems of forest trees, because of the difficulty and time involved in excavation, have received less attention and study than have those parts of trees which grow above ground. Relatively little is known concerning the growth and development of the root systems of most of our native trees; and for many species such information is lacking or not strictly accurate. In the Rocky Mountain region, lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) is an important species and subject to relatively intensive management, yet information is very meagre concerning its root system.

Much of the evidence which has been gathered concerning root systems appears contradictory. In part this can be accounted for by the fact that no other organ of a tree varies as much in its development as does its root system. Many investigators have drawn their conclusions from observations of the root system of one tree or of a few trees, because of the difficulty in excavating the roots. This accounts for some of the contradictions in root literature.

There appears to be a great difference in the plasticity of the root systems of different species (Pulling 1918), some being able to modify greatly their development on different soil types while others are quite rigid. This flexibility is of considerable importance in determining the range of sites upon which a species can succeed. Toumey (1929) has shown that the initial root habit is often the determining factor in the survival and establishment of an individual tree.

Though the roots of trees are of considerable importance in forestry, study of them has been largely neglected in the past. Silvicultural operations, to a great extent, achieve their benefit to a forest through their effect upon the root systems of the trees. Sufficient knowledge of the root systems will in the future place cutting, thinning, and planting methods upon a more scientific basis than they are today. Magyar (1929) states that, "If we want, therefore, to give a scientific basis to silviculture, it will be our first duty to examine systematically the root system of the trees on different sites."

These studies were undertaken to obtain as much information as possible concerning the growth and development of the root systems of juvenile lodgepole pine, in the hope that the data obtained would lead to conclusions which could be applied to the management of this species. The entire summers of 1939 and 1940 were devoted to the excavation and measurement of the root systems of some 105 lodgepole pines, which ranged from 1 to 15 years in age.

The plan of study included the careful excavation of the entire root system, mapping this as it was uncovered, and measuring the number and length of roots of each order. Seventy of the root systems were carefully arranged on a grid in as near natural positions as possible and photographed. Oven-dry weights of tops and roots for each tree excavated were determined later in the laboratory. Statistical analyses were made where an important relationship of factors was indicated.

DESCRIPTION OF SITES

The excavations were carried out at two different lodgepole pine sites in the vicinity of the summer camp of the Division of Forestry of Colorado State College at Pingree Park, Colorado.

The site designated hereafter as Pingree Park was a fire lane from 30 to 60 feet wide which was constructed in 1916 to protect the camp from fire. Prior to 1894 this area had supported an overmature forest of lodgepole pine, with some ponderosa pine and Douglas fir on the warmer aspects. In that year it was burned by a large forest fire which devastated much of the surrounding country. Following the fire, this area developed into a dense, almost pure, stand of lodgepole pine. In 1939 the fire lane supported an open, scattered mixture of herbs, shrubs, and young lodgepole pines. The ground cover density, in tenths, for a 3-foot radius about each of the 70 excavated seedlings ranged from 0.1 to 0.9 with a mean of 0.49. It was noted that the lodgepole seedlings occurred in open places or under aspen, but not in the heavy grass. Many of these growing in the open were not doing well as evidenced by yellowish needles, the dying back of the top, or the lack of new growth. The most vigorous seedlings were those growing near to and shaded by aspen. The elevation of the fire lane was 9,100 feet and it sloped down toward the north at a rate varying from 0 to 12 degrees, with a mean slope of 3.4 degrees. This area is characterized by an abundance of rainfall and heavy winter snows. The summers of 1939 and 1940 were abnormally dry, with only occasional con-

vectional showers which occur in normal years almost daily.

The soil on this site was carefully analyzed. At each of four locations samples were taken at depths of 0 to 3 inches, 11 to 13 inches and 23 to 25 inches; and in addition, at depths of 35 to 37 inches and 47 to 49 inches from one location. There was no soil profile visible, the material being of glacial morainic origin and undifferentiated.

The percentage of sand, silt and clay was determined by the Bouyoucos (1935) hydrometer method, after the gravel had been removed by passing the material through a 2 mm. sieve. This method, which is based on the rate of sedimentation, gives results within 5 percent of accurate. The findings of these determinations are presented in Table 1.

The large variation in the amount of gravel, as indicated in Table 1, is typical of the area on which the excavations were made. There were small pockets of high gravel content scattered throughout the soil profile.

The percentages of sand, silt and clay separates are fairly uniform, although there is some variation with different depths. The silt and clay separates combined range between 24.81 and 8.00 percent at the Pingree Park site. On the basis of textural grade, the soil samples from the Pingree Park site are classified either as "gravelly sandy loams," or, for the samples where the percentage of silt and clay combined is less than 20 percent of the material, as "gravelly sands" (Lyon & Buckman 1934).

The soil samples were further analyzed to determine nutrient conditions, acidity and total amount of organic matter present. Morgan's Universal Soil Testing System (Morgan 1937) was used to determine the amounts of nitrate nitrogen, ammonia nitrogen, potassium, and calcium. The phosphorus

was determined by the buffer acetate method of Dahlberg and Brown (Dahlberg & Brown 1938). the pH was determined by the glass electrode method. The total amount of organic matter present was found by roasting oven-dried samples of soil to a red-hot color and then determining the difference in weight before and after roasting. Results of these tests are shown in Table 2.

Interpreting these results, the pH is found to be definitely but not extremely acid, ranging from 5.25 to 6.35.

Nitrate nitrogen is considered low if the test shows 5 parts per million (p.p.m.) and very low if only 1 part per million. The soil tested was very low. This may in part account for the abundant mycorrhizae present on the roots (Melin 1922, Hatch & Doak 1933).

Ammonia nitrogen ranging in the above tests from 5 to 20 p.p.m., was apparently present in sufficient quantities. Morgan lists 25 p.p.m. as medium high, 10 p.p.m. as medium and 5 p.p.m. as low. In all cases surface samples tested better than low.

Potassium is considered high when 200 p.p.m. are present, medium with 100 p.p.m., and low with 75 p.p.m. All samples above 23 inches tested from medium to high.

Phosphorus with one exception (and this surface sample was taken on the site of an old brush burn and contained some charcoal) tested from 0.31 to 0.11. Since any reading below 0.6 is considered deficient, phosphorus is seriously lacking in this location.

Calcium varies greatly in the amount present, ranging from high to very low. 1,000 p.p.m. is rated as medium high, 500 p.p.m. as medium, 375 p.p.m. as low and 250 p.p.m. as very low. As sufficient calcium was present in some layer at each location

TABLE 1. Percentages of gravel, sand, silt, and clay present in soil samples.

A. PINGREE PARK SOIL SAMPLES

Depth Inches	Sample A Percentages of				Sample B Percentages of				Sample C Percentages of				Sample D Percentages of			
	Gravel	Sand	Silt	Clay	Gravel	Sand	Silt	Clay	Gravel	Sand	Silt	Clay	Gravel	Sand	Silt	Clay
0– 3...	23.1	53.1	18.4	5.4	29.1	46.1	19.8	5.0	34.2	43.2	17.7	5.0	48.9	34.6	13.9	2.6
12...	33.9	45.9	14.0	4.2	62.1	26.7	5.2	3.0	52.3	34.3	10.2	3.2	24.8	51.5	19.0	4.7
24...	34.5	45.8	13.9	5.8	40.4	36.8	12.7	9.9	61.9	30.1	6.3	1.3	16.5	68.5	9.1	5.9
36...	....	....	....	....	....	....	....	....	....	....	....	....	62.3	30.8	5.6	1.3
48...	....	....	....	....	....	....	....	....	....	....	....	....	45.0	45.5	6.0	1.4

B. HOURGLASS LAKE SOIL SAMPLES

Depth Inches	Sample A Percentages of				Sample B Percentages of				White Sand Layer (15-18″) Percentages of			
	Gravel	Sand	Silt	Clay	Gravel	Sand	Silt	Clay	Gravel	Sand	Silt	Clay
0– 3.....	49.6	46.0	2.7	1.7	92.6	6.5	0.7	0.2	....	....	....	....
6.....	80.4	16.4	0.9	0.3	70.5	27.5	1.5	0.6	....	....	....	....
12.....	25.0	67.0	5.5	2.0	40.3	34.5	4.4	0.8	15.8	72.8	9.5	2.0
24.....	....	....	....	....	32.8	60.3	6.2	0.7	....	....	....	....

TABLE 2. Amounts of nutrients, pH, and total organic matter present in soil.

A. PINGREE PARK

Location	Depth in Inches	pH	Nitrate Nitrogen p.p.m.	Ammonia Nitrates p.p.m.	Potassium p.p.m.	Phosphorus p.p.m.	Calcium p.p.m.	Percentage of Total Organic Matter
A	0–3	5.3	Low	Medium	Medium	Low	Very Low	2.02
	11–13	5.7	Very Low	Low	Medium	Low	Very Low	1.42
	23–25	5.7	Trace	Low	Low	Very Low	Medium	1.41
B	0–3	6.2	Trace	Medium	High	Medium	Med. High	4.54
	11–13	6.5	Trace	Low	Medium	Low	Very Low	1.00
	23–25	6.4	Trace	Low	Low	Low	Med. High	1.62
C	0–3	5.9	Very Low	Med. Low	Medium	Low	Medium	4.90
	11–13	6.0	Very Low	Low	Medium	Low	Very Low	1.65
	23–25	5.9	Trace	Low	Medium	Low	Very Low	1.24
D	0–3	6.1	Very Low	Med. Low	High	Low	High	4.51
	11–13	6.1	Trace	Low	Medium	Low	Low	1.57
	23–25	6.2	Trace	Low	Medium	Very Low	Med. High	1.68
	35–37	6.2	Trace	Low	Low	Very Low	Med. High	1.31
	47–49	6.2	Trace	Low	Low	Very Low	Very Low	1.09

B. HOURGLASS LAKE

Location	Depth in Inches	pH	Nitrate Nitrogen p.p.m.	Ammonia Nitrates p.p.m.	Potassium p.p.m.	Phosphorus p.p.m.	Calcium p.p.m.	Percentage of Total Organic Matter
A	0–3	5–6	Very Low	Low	–	Low	Med. Low	–
	5–7	5–6	Low	Low	–	Low	Low	–
	11–13	5–6	Low	Low	–	Medium	Very Low	–
B	0–3	5–6	Very Low	Low	–	Low	Very Low	–
	5–7	5–6	Very Low	Very Low	–	Med. Low	Very Low	–
	11–13	5–6	Low	Low	–	Medium	Very Low	–
	23–25	5–6	Trace	Low	–	Medium	Absent	–
White Sand	15–18	5–6	Low	Low	–	Medium	Very Low	–

where the soil was tested, this condition cannot be considered critical.

These tests indicate that the soil would be classed as poor. While not seriously lacking in ammonia nitrate, calcium, and potassium, other essential plant foods such as nitrate nitrogen and phosphorus are not present in sufficient quantities.

The site designated hereafter as Hourglass Lake was selected because of the great contrast it offered to the Pingree Park site. Situated two and one-half miles northwest of Pingree Park, it was located in a large cut several acres in extent, where for a depth of 3 to 4 feet the soil, almost pure sand and gravel, had been excavated to build a reservoir dam. This construction had taken place some twenty years prior to this study and the cut contained many lodgepole seedlings and saplings. These were growing under conditions of practically no competition, as evidenced by the fact that the ground cover density, in tenths, for a 3-foot radius around each of the 35 excavated seedlings ranged from 0 to 1/5 of 1/10 with a median of less than 1/20 of 1/10.

The area surrounding the cut contained a forest of overmature unmerchantable lodgepole, indicating very definitely a class four site. This cut was practically level, the slope varying only from 0 to 4 percent, and was at an elevation of 9,500 feet. The precipitation was comparable to that of Pingree Park.

Soil samples were taken from two locations within the cut at depths of 0 to 3, 5 to 7, 11 to 13, and at depths of 15 to 18, and 23 to 25 inches at one location, and analyzed by the same methods used at the Pingree Park site. The results are shown in Tables 1 and 2, and indicate that this site is very poor and definitely deficient in the essential plant foods. The fact that lodgepole pine seedlings were able to survive in this site indicates a remarkable tolerance to soil conditions.

METHODS OF COLLECTING AND COMPILING DATA

FIELD STUDIES

Before excavating each tree, certain features of the site were recorded. The aspect and slope were noted, and the ground cover for a radius of 3 feet from the tree stem was mapped, recorded by species present and estimated as to cover density to the nearest tenth. If large rocks, logs, stumps, or other factors were present within the 3-foot radius which would have an effect on the root system, they were indicated on the map.

The top was cut at the root collar and the follow-

ing measurements taken: total height, total height above ground at the end of each year's growth, length of the growth of the current season, diameter at the root collar, and average length of the needles. The ages were determined microscopically from sections taken at the root collar and stained with a combination of phloroglucinol and hydrochloric acid. When necessary this method was also used to determine the extent of a year's growth, because, as lodgepole pine is multinodal (Shaw 1914), it is often impossible to determine the growth of a year from the branch whorls. The tops were then placed in labeled sacks for further study.

Before actual excavation, the area over the root system was divided into quadrats by wires running north and south and east and west, and intersecting above the root collar. Excavation was then made and recorded by quadrats and by 3-inch-depth zones.

The method of excavation, evolved after considerable trial and error, proved very satisfactory. Pressure sprayers of the type used in orchards were adjusted so that a very fine stream of water was ejected with considerable force. With the use of a screwdriver to loosen pebbles, roots and other heavy objects and a sprayer to wash out the roots, the entire system was uncovered with a minimum of damage. It was found that even mycorrhizal roots were left intact and could be quite accurately counted. For the deeper roots it was necessary to dig a well or trench at some distance from the roots in order to get the needed drainage.

In addition to being the most accurate method developed, this procedure was relatively rapid. It was possible for one man to excavate, measure and record as many as three or four 1-year-old seedlings in a day. As the age increased, however, the amount of time required was much greater. For example, it took one man five weeks to excavate, measure and record the root system of a 15-year-old tree.

The field measurements of the root systems were recorded by quadrats and 3-inch depth zones. The lengths of the taproot, primaries, secondaries, and all other root orders, which are classed as tertiaries in this study, were carefully measured. In addition all roots less than one-half inch in length were classed as short roots and counted, and the average figure of their length was determined. The number of mycorrhizae were likewise counted. In the case of those which were dichotomously branched each branch was considered a mycorrhiza. The growing tips, separated into large (over one-fourth inch long) and small, were also recorded. In the pine these are very conspicuous during the growing season, being clear white. They serve as a measure of the time of root growth, for on vigorously growing roots they may be several inches in length when growth is rapid.

Care was taken to record all the peculiarities observed in the development of the roots, such as growth in decayed roots and changes in the root system. In one location a trench was made in order to bisect the root system of a 15-year-old lodgepole pine sapling, and a map of all roots in the soil profile was made.

As the root system was excavated, it was carefully mapped on graph paper, both the horizontal and vertical extent being shown. The root systems excavated during the first summer were, in addition, placed on a 3-inch grid in as near natural position as possible and photographed from a special scaffold. This was not continued the second summer, as it was felt that the value of the pictures did not warrant the time spent in obtaining them. The roots were then stored in sacks for later study.

LABORATORY METHODS

The oven-dry weights of the roots, the needles, and the woody portions of the crown were carefully determined. The specimens were dried at 99° C. until all decrease in weight had ceased. They were then weighed to the nearest 0.01 gram.

Seeds were planted in the laboratory in a glass-sided box and certain measurements of early growth and development were recorded. Later the oven-dry weights of roots, stems, and needles were determined. Fresh root systems were excavated and carefully drawn to scale to show the typical macroscopic features.

STATISTICAL STUDIES

The data collected for the 105 excavated pines were tabulated in summary form and subjected to study. Several graphs were drawn from these data, which were fitted by the least squares method. This method gives the best fitted curve possible among the class of curves assumed to explain the data, as it minimizes the sum of the square of each deviation of the plotted points from the curve. The formula used to determine the point values by the "least squares" method is:

$$\sum_{x=1}^{15} \sum_{j=1}^{Nx} Y_{xj} - AN - B\sum N_x x - C\sum N_x x^2 = 0$$

$$\sum_{x=1}^{15} \sum_{j=1}^{Nx} XY_{xj} - A\sum N_x x - E\sum N_x x^2 - C\sum N_x x^3 = 0$$

$$\sum_{j=1}^{15} \sum_{j=1}^{Nx} X^2 Y_{xj} - A\sum N_x x^2 - B\sum N_x x^3 - C\sum N_x x^4 = 0$$

where x = the experimental value on the horizontal scale,

y = the experimental value on the vertical scale,

N = the number of observations, and

j = any particular tree in one of the age classes.

The values of A, B, and C are to be solved for, and the points on the corrected, "least squares" curve are then equal to:

$$Y_{xj} = A - Bx - Cx^2$$

where Y_{xj} equals the correct curve point.

In a few cases these formulas give slightly minus values for the 1-year-old age class. Rather than plot these minus values, the curves were rounded off to zero from the 2-year-old age class. This is justified by the small possible error, as all these 1-year-old values are relatively minute.

The coefficient of correlation, symbolized as r, was calculated to determine if there is a significant degree of association existing between the age of the tree and the length of the roots and between the height of the top and the length of the roots. The formula used is:

$$r = \frac{N\sum xy - \sum x \sum y}{\sqrt{(N\sum x^2 - [\sum x]^2)(N\sum y^2 - [\sum y]^2)}}$$

where x = age or total top height of individual tree,
    y = total linear length of individual root system, and
    n = number of trees measured.

To determine whether there is a significant difference in the top-root ratio between the two sites, the value of t was calculated. This determination is achieved by setting up the hypothesis that the true average top-root ratio for all trees on one site is equal to that on the other site. If t is equal to a figure slightly greater than the standard deviation, this hypothesis is rejected and a significant difference

is found to exist. The formula $\quad t = \frac{|\bar{x}_1 - \bar{x}_2|}{S'}\sqrt{\frac{N_1 N_2}{N_1 + N_2}}$

is used where $S' = \sqrt{\dfrac{N_1 S_1{}^2 + N_2 S_2{}^2}{N_1 + N_2 - 2}},$

    S = standard deviation,
    $\bar{x}$ = arithmetic mean of top-root ratios, and
    n = number of trees measured.

STUDIES UNDERTAKEN AND RESULTS OBTAINED

TOP DEVELOPMENT

Top development between the two sites varied but little during the 10-year period of growth represented by trees excavated for this study. Total height, diameter at root collar, and average needle length were slightly larger on the Hourglass Lake site than on the Pingree Park site (Figs. 2, 3, and 4). There was a greater difference in the oven-dry weights of the tops, both needle weight and woody crown weight showing a much sharper increase with age at the Hourglass Lake site (Figs. 5 and 6). This is somewhat surprising as the Hourglass Lake site is definitely the poorer of the two sites, as evidenced by soil analyses and the fact that the surrounding forest indicates a class four site while at Pingree Park the mature trees indicate a class two site. The explanation for this increased top growth at the Hourglass Lake site undoubtedly lies in the almost complete freedom from competition at this location, whereas the soil profile (Fig. 1) taken at the Pingree Park site indicates that root competition must be quite severe.

EXTENT OF ROOT SYSTEMS

The extent of root development was considered for depth, length of roots, number of roots, the hori-

DEPTH IN INCHES	WOODY ROOTS ○ HERBACEOUS ROOTS •	STEM OF PINE	WOODY ROOTS NUMBER	PERCENT	HERBACEOUS ROOTS NUMBER	PERCENT
0			72	34.3	209	55.7
3			47	22.4	54	14.4
6			41	19.5	32	8.5
9			20	9.5	24	6.4
12			10	4.8	30	8.0
15			6	2.9	7	1.9
18			4	1.9	7	1.9
21			6	2.9	4	1.0
24			1	0.4	7	1.9
27			3	1.4	1	0.3
30			210	100.0	375	100.0

DISTRIBUTION OF ROOTS BY THREE-INCH-DEPTH ZONES

LENGTH IN INCHES
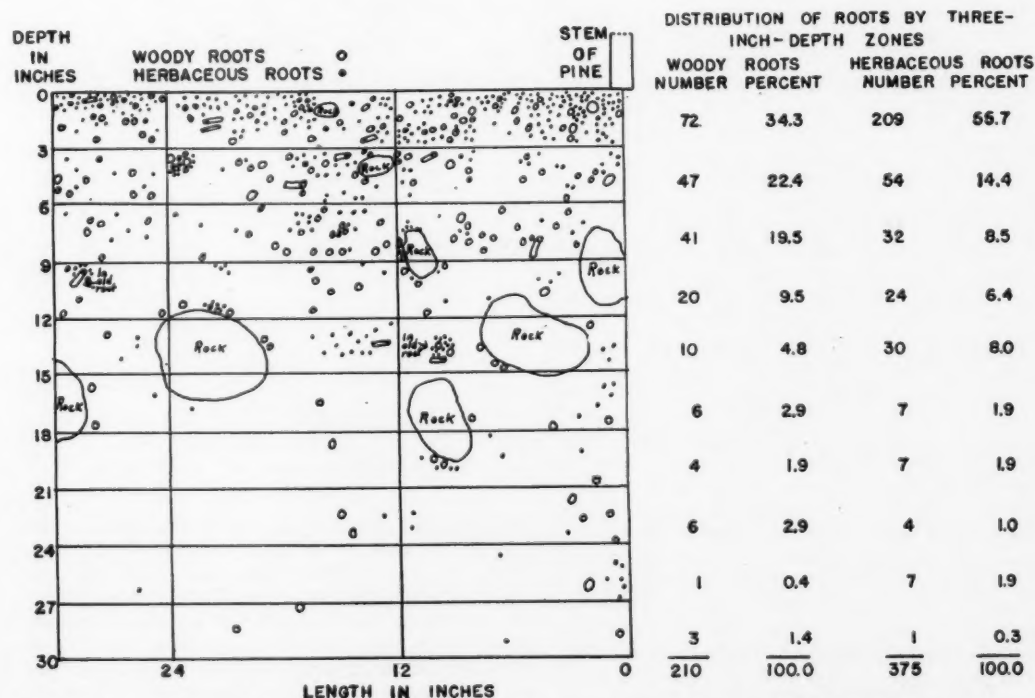
FIG. 1. Transect showing distribution of roots in the soil near one 15-year-old lodgepole pine.

zontal area occupied by the roots, number of growing
tips, and number of mycorrhizae.

DEPTH

In Figure 7 the maximum depths reached by the
roots for each age class have been plotted. It is
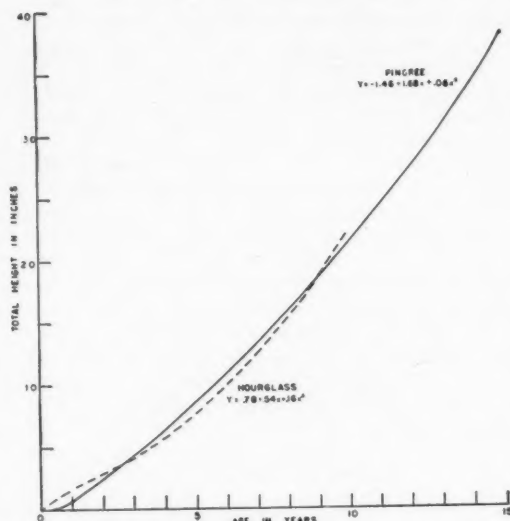
FIG. 2. Total height over age.
$$Y = A + B_x + C_{x^2}$$

FIG. 4. Average length of needles over age.
$$Y = A + B_x + C_{x^2}$$

FIG. 3. Diameter at root collar over age.
$$Y = A + B_x + C_{x^2}$$
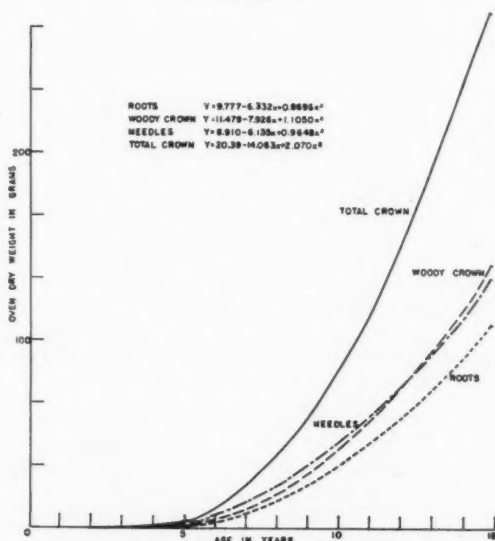
FIG. 5 Oven-dry weight over age, Pingree.
$$Y = A + B_x + C_{x^2}$$

apparent that there is a radical difference in the
vertical development of roots between the Pingree
Park and the Hourglass Lake sites. This is even
more strikingly brought out in Table 3 which shows
the percentage of total root length present in each
3-inch depth zone. In both sites the majority of the
roots are in the upper few inches of soil, but the
average root depth is much greater at the Pingree
Park site. It is striking that 62 to 80 percent of

all roots occur in the upper 3 inches of soil at the Hourglass Lake site. The average depth of roots,
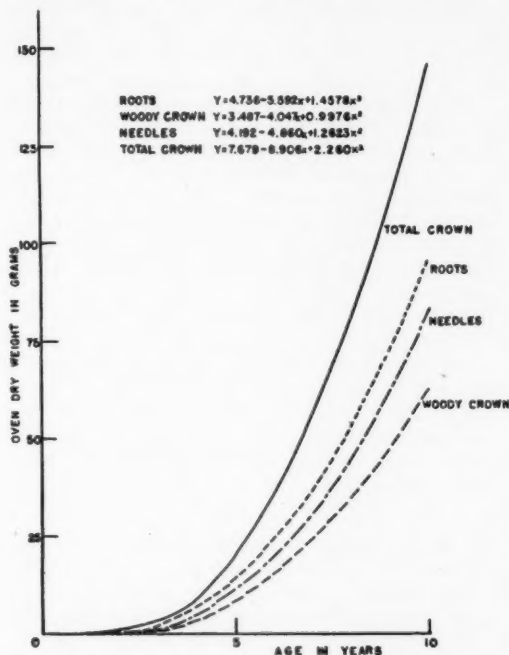
FIG. 6. Oven-dry weight over age, Hourglass.
$$Y = A + B_x + C_{x^2}$$
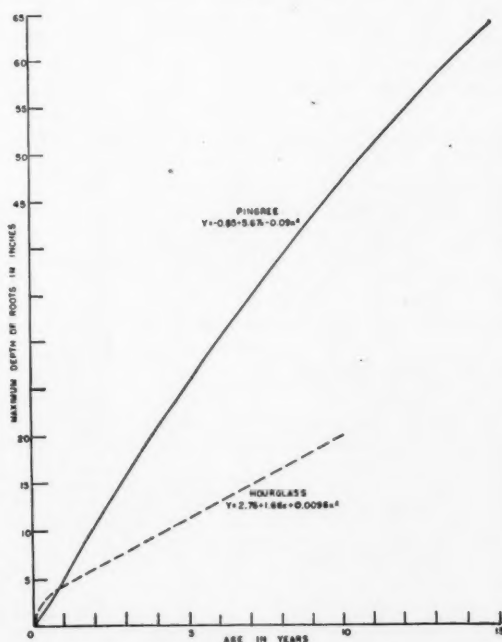
FIG. 7. Maximum depth of roots over age.
$$Y = A + B_x + C_{x^2}$$

on both sites, shows a definite trend toward increase with age. These data indicate that the vertical development of the root system of lodgepole pine is markedly affected by the soil type and agree with the conclusion of Laitakari (1927) that the shallowest root systems are in sandy soils.

TABLE 3. Percentages of total root length in 3-inch depth zones.

PINGREE PARK						
Depth Zone	1 yr.	2 yr.	3 yr.	4 yr.	10 yr.	15 yr.
Inches						
0 - 3.....	63	72	64	77	48	36
0 - 6.....	90	89	76	86	67	47
0 - 9.....	95	95	83	91	71	52
0 - 12....	100	97	90	92	75	57
0 - 24....	...	100	97	96	85	68
0 - 36....	...	...	100	98	93	78
0 - 48....	...	...	...	100	98	82
0 - 60....	...	...	...	...	100	90
0 - 72....	...	...	...	...	...	100

HOURGLASS LAKE					
Depth Zone	1 yr.	2 yr.	3 yr.	4 yr.	10 yr.
0 - 3.............	80	67	70	71	62
0 - 6.............	100	97	99	89	88
0 - 9.............	...	100	100	98	92
0 - 12............	...	...	...	100	94
0 - 24............	...	...	...	...	99
0 - 36............	...	...	...	...	100

It was noted that almost without exception the main lateral roots appeared from the upper 3 inches of the tap-root and for the most part remained shallow. These large laterals, usually fewer than six in number, made up the greatest percentage of lateral root growth.

At the Pingree Park site it was noted that the tap-root is normally strongly developed in lodgepole pine and that a graph of the depth of the tap-roots proceeds in an almost linear manner for the first 15 years of the tree's life. In ten instances, because of solid rock or other mechanical obstructions, the tap-root was unable to develop normally. In such cases, one or more of the main lateral roots would branch and send one fork vertically downward to approximately the same depth that the tap-root would have been expected to reach. The photograph of the vertical distribution of the roots of tree number 59 (Fig. 8) is typical of this development. Frequently one or more of the laterals would branch and send one fork down vertically even though the tap-root system was well developed.

To obtain a better understanding of the vertical distribution of roots, a transect was made through a part of the root system of a 15-year-old lodgepole pine on the Pingree Park site (Fig. 1). A vertical trench was dug with the top of the tap-root at one corner. All roots within a 30-inch square from the top of the tap-root were mapped by 3-inch depth zones, herbaceous roots being separated from woody roots. The numbers and percentages of roots in each
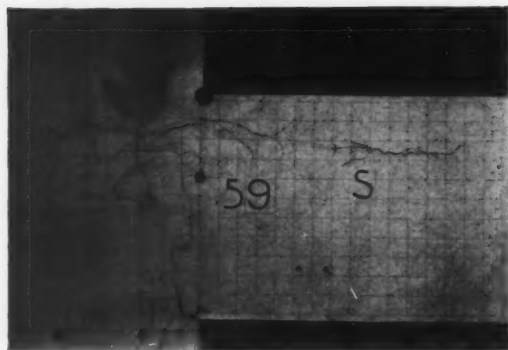
FIG. 8. Photograph of the root system of tree number 59, an 8-year-old tree from the Pingree Park site.

depth zone are shown. Even though this transect included approximately one fourth of the tap-root system, it is noteworthy that the major number of both herbaceous and woody roots appeared in the upper 6 inches of soil. The distribution of the roots through the soil was not uniform, there being rather large areas where no roots occurred while in other areas the roots were crowded.

This study would indicate that, contrary to common opinion, lodgepole pine, at least in early life, cannot be considered a shallow-rooted tree. The depth to which the roots descend depends on the soil type.

The factor or factors causing the suppression of vertical root development at the Hourg'ass Lake site were less clearly defined but appeared to be correlated with soil moisture. This would agree with the conclusions of Tolskii 1913; Cannon 1914, 1915, 1917, 1918; Haasis 1921; and Magyar 1929. The very loose soil could not hold much moisture for a long period of time, yet it appeared as though the roots depended on the frequent showers for their moisture. Occasional dead roots of large trees indicated that roots had penetrated to a considerable depth prior to the removal of the surface layer and that any mechanical difficulty of penetrating through the sand and gravel could not account for the shallowness of the roots. The map of 4-year-old tree number 75 (Fig. 9) is a typical example of root development at this site. In most cases the tap-root would start out strongly but taper off and become suppressed in a very few inches. A copious branching from the small downward growing laterals was common.

Of the 35 trees excavated on this site, only two 10-year-old trees had roots which penetrated to a depth greater than 12 inches. In the case of both of these trees all the deep roots followed old decaying roots. The roots on two other 10-year-old trees did not grow deeper than 12 inches and no old roots were observed near them. One of the two trees with deep roots had a peculiar development which clearly indicated the dependence of root growth on soil type and soil moisture. Under this tree, at a depth of 15 to 18 inches, was a nearly horizontal layer of fine white sand, very different in appearance from the rest of

the soil. This layer varied from about one-half inch to 3 inches in thickness and through it had grown a portion of the root system which covered nearly as large an area as that of the surface layers. The roots had reached this layer by following down an old root system and had then grown out through it in every direction. This agrees with the conclusions of Hooker (1915) that roots turn toward moisture in the soil but will not penetrate a dry layer of soil to reach a moist layer farther away. At no point did the roots grow above or below this layer, and the fact that 1,682.1 inches of roots were measured in it indicates the extent to which they spread. These roots differed from those near the surface in that they had very few branches and almost no short roots or mycorrhizae. (At this depth mycorrhizae were found only in or near decaying old roots). Samples of this layer were later analyzed in the laboratory; as no higher fertility was evidenced (Tables 1 and 2) it appeared that the finer texture enabled it to hold water percolating down from above, and that this increased soil moisture was the stimulus for the extensive root growth.

LENGTH

In Figure 10 the total length of roots for each age class has been plotted for both sites. The difference in total length between the two sites is almost as radical as is the difference in maximum depth. This graph substantiates the conclusions of several investigators that as a site becomes poorer, root develop-
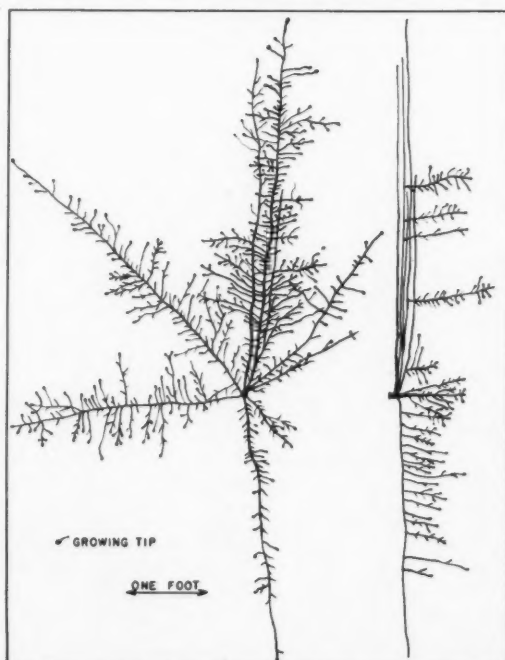
FIG. 9. Graph showing horizontal and vertical development of the root system of tree number 75, a 4-year-old tree from the Hourglass Lake site.
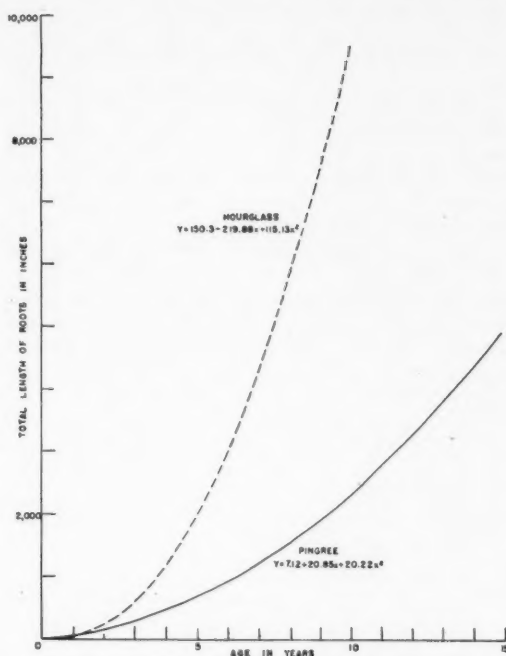
FIG. 10. Total length of roots over age.
$$Y = A + B_x + C_{x^2}$$

ment is increased (Savitz 1882, Ter-Sarkisov 1882, Tolskii 1913, Markle 1917, Weaver 1919, Aaltonen 1920, Haasis 1921, Busgen and Munch 1926, Hilf 1927, Laitakari 1929, Stevens 1931, Heyward 1933, and McQuilken 1935). It appears to contradict the findings of Moore (1922), Baker and Korstian (1931), and Turner (1936b).

These curves show that there is little difference in total root length between the sites until after the second year. From the third year on, increase in total root length at the Hourglass Lake site was very rapid and proceeded in an almost linear manner, the rate of increase greatly exceeding that of the Pingree Park site. It took the root system at the Hourglass Lake site approximately seven and one-half years to grow the 4,905 inches average of the 15-year-old trees at the Pingree Park site.

In order to determine whether this greater root growth at the Hourglass Lake site was evenly distributed throughout the lateral root system, the length of the long primaries at both sites was compared (Fig. 11). The results of this curve are interesting. They indicate first, that in this regard there is no significant difference between the sites; secondly, that the rates of increase are practically parallel; and lastly, that the rate of increase is a linear one; hence it may be maintained by trees of greater age than those excavated. This proves that the much greater root development at the sterile Hourglass Lake site lies in the greater branching of the lower orders of roots in the root system.

A study of the average number of long and short roots of the different orders further substantiates this conclusion. In Table 4 it is apparent that there is little difference in the number of long and short primary roots between the two sites; nor is there any marked difference in the number of long and short secondary and tertiary roots until after the third year. Thereafter, however, the difference in the number of both long and short roots is great.

TABLE 4. The average number of roots for certain age classes.

Age Class	Site	NUMBER OF ROOTS					
		Primary		Secondary		Tertiary	
		Long	Short	Long	Short	Long	Short
1	Pingree Park.......	8.6	23.2	0.9	65.7	0.0	35.6
	Hourglass Lake	9.3	14.9	5.2	73.9	0.2	12.5
2	Pingree Park.......	9.7	20.4	2.9	117.7	0.2	63.3
	Hourglass Lake	18.9	29.3	26.6	244.0	3.6	102.3
3	Pingree Park.......	17.5	44.6	38.1	307.3	12.6	333.9
	Hourglass Lake	27.3	27.5	83.3	266.8	28.4	284.6
4	Pingree Park.......	29.6	19.8	89.6	311.6	17.4	476.7
	Hourglass Lake	18.4	22.6	222.0	487.0	214.6	1,011.0
10	Pingree Park.......	49.8	6.8	309.4	513.2	267.2	2,094.6
	Hourglass Lake	32.0	15.8	737.3	817.5	3,141.3	7,961.8

The correlation coefficient, which measures the degree of association between two variables, was computed to determine the closeness of the relationship existing between the age in years and the total linear
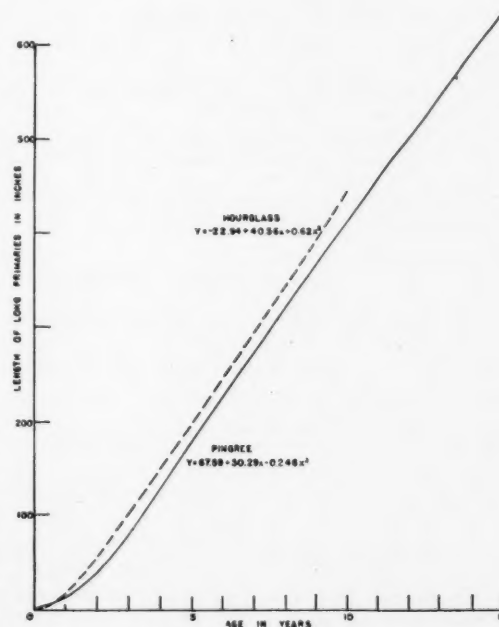
FIG. 11. Length of long primaries over age.
$$Y = A + B_x + C_{x^2}$$

length of root systems. The formula used to determine this correlation coefficient (symbolized by r) is:

$$r = \frac{N\sum xy - \sum x \sum y}{\sqrt{(N\sum x^2 - [\sum x]^2)(N\sum y^2 - [\sum y]^2)}}$$

where x = age of individual tree,

y = total linear length of individual root system, and

N = number of trees measured.

The correlation coefficient for the Pingree Park data is 0.8628; and for the Hourglass Lake data it is 0.9184. Perfect correlation of age and root length would give r a value of 1.0, while complete lack of correlation would give r a value of 0 (Leonard & Clark 1939). The high value of r obtained from the data at both sites shows that there is a strong relationship and indicates that a knowledge of age would make possible a prediction of root length, particularly an average for a given age rather than for an individual tree.

By applying the following formula, it can be determined with reasonable certainty that the true, total linear length of the root system of a given tree will fall between certain limits:

$$\text{Est. } y - y = r \frac{S_y}{S_x}\left(X - \bar{x}\right)$$

where $S_y = \frac{1}{N}\sqrt{N\sum y^2 - (\sum y)^2}$,

$S_x = \frac{1}{N}\sqrt{N\sum x^2 - (\sum x)^2}$,

Est. y = root length of a certain tree which has not been excavated,

X = age of the unexcavated tree,

y = total linear length of root system of individual tree,

$\bar{y}$ = arithmetic mean of length of root system,

x = age of individual tree,

$\bar{x}$ = arithmetic mean of age, and

N = number of trees measured.

The true, total linear will fall between the limits indicated in the following equation:

$$\text{Est. } y - 1.96 S_y \sqrt{1-r^2} < \text{true y value} < \text{Est. } y + 1.96 \; S_y \; \sqrt{1-r^2}$$

These limits may be large when applied to an individual tree; however, if they are applied to N number of trees the true average y value will be reduced in proportion to the site of N. So:

$$\text{Est. } y - \frac{1.96 \; S_y \sqrt{1-r^2}}{\sqrt{N}} < \text{true average y value for N trees of a given age} < \text{Est. } y + \frac{1.96 \; S_y \sqrt{-r^2}}{\sqrt{N}}$$

This method of determining the limits within which the root length of a tree would fall was applied to the Hourglass Lake data. No 9-year-old trees were excavated at this site and the estimated total length of the root system of a single tree of this age was calculated. The estimated total length was found to

be 7,433.14 inches (this agrees almost exactly with the value on the curve plotted by the "least squares" method (Fig. 8). The limits within which the length of a single root system of a 9-year-old tree might be reasonably certain to fall are between 4,999.89 inches and 9,866.39 inches. These limits are very large and might prove of little actual value. However, if total average root length for 100 nine-year-old trees were desired, it would be found to fall between 7,189.81 inches and 7,676.47 inches.

Age is not always easy to determine in the field for young trees. For this reason total top height was studied to ascertain if this easily measured factor could be used as a reliable indicator of total root length. The curve (Fig. 12) resulting from plotting
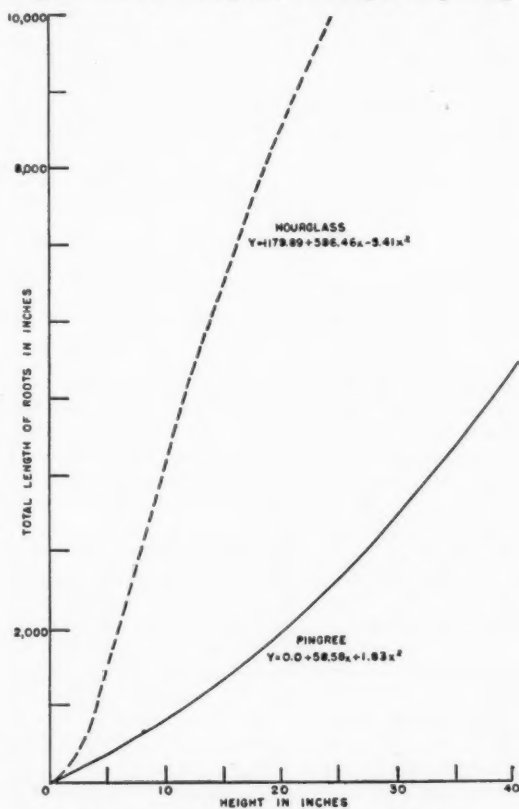
FIG. 12. Total length of roots over height.
$$Y = A + B_x + C_{x^2}$$

the total length of the root systems over the total top heights, while indicating a slightly more linear correlation, is not very different from the curve of total root lengths over ages (Fig. 10). As a further test the coefficient of correlation was calculated to measure the closeness of the relationship of total top height to total root length. This was found to be 0.9176 for the Pingree Park data and 0.9528 for the Hourglass Lake data. These values show a very strong relationship between total top height and total
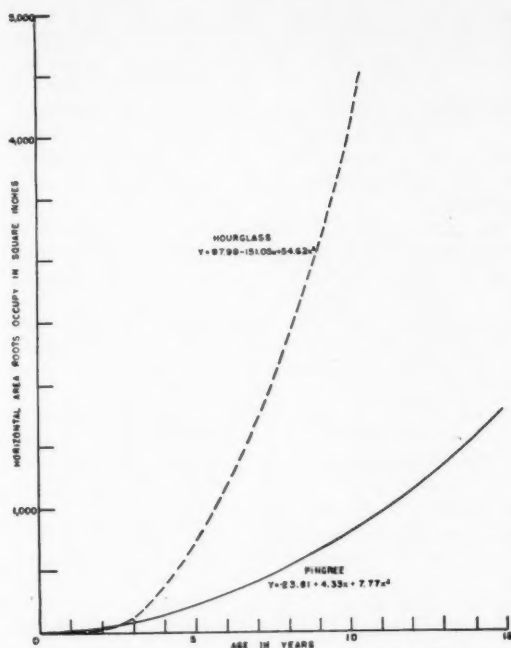
FIG. 13.　Horizontal area roots occupy over age.
$$Y = A + B_z + C_{z^2}$$

root length and indicate that total top height gives a better estimate than age of total root length.

The same formula can be used to determine the limits within which the true, total linear root length of a tree of any given total height will fall.

HORIZONTAL AREA

From the field maps of each excavated root system, the horizontal areas occupied were determined by use of a planimeter. Each root system was traced around by three separate readings, the recorded area being the average of these readings. As would be expected, the graph curves (Fig. 14) of the horizontal root area closely simulate the curves for the total length over
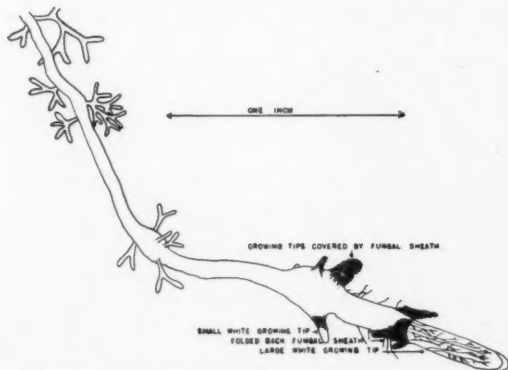
FIG. 14.　Sketch of root excavated April 13, 1940.

age, and the great influence of the different sites is clearly shown. As in the case of total length, the rate of increase for the Hourglass Lake site is not markedly greater than that of the Pingree Park site until after the third year.

TABLE 5.　Average horizontal areas occupied by roots in square inches.

Age Class	1	2	3	4	5	6
Pingree Park.....	6.9	12.1	58.5	148.6	131.1	244.8
Hourglass Lake...	4.6	14.0	38.2	461.5	.....	.....

Age Class	7	8	9	10	15
Pingree Park......	304.3	277.2	955.6	717.4	1,768.3
Hourglass Lake...	.....	.....	.....	4,033.4	....

FACTORS INFLUENCING THE GROWTH AND DEVELOPMENT OF ROOTS

A study of the horizontal and vertical spread of the root systems clearly shows that there is no definite symmetry of development, such as is characteristic of the above-ground portion of young lodgepole pine. While it is true that there is a typical tap and lateral root development which is generally present, little more can be prophesied regarding a root system before it is excavated. A number of factors are responsible for this lack of uniformity in development, some of which are readily apparent and others difficult to discern. The following factors seem to have a distinct influence upon root development.

PRESENCE OF DECAYED OR DECAYING ROOTS IN THE SOIL

The results of this study indicate that one of the major factors influencing the development of root systems of young lodgepole pine is the presence in the soil of old roots. These decaying roots were frequently permeated with numerous living roots (Fig. 1). Many shallow lateral roots and the majority of deep-growing lateral roots were confined to the location of these old roots, and frequently the tap-root system would be deflected to an area of old-root penetration. Often the living roots would remain entirely within a partially decayed root for several feet. In no case were mycorrhizae noted at any considerable depth from the surface, except in places where the roots followed the old root channels. Several previous investigators have noted this relationship between root development and the root systems of former trees (Savitz 1906; Laitakari 1929; Cheyney 1929, 1932; Pessin 1939).

In a few cases there was a remarkable ramification of roots within an old larger root, the lateral and its branches all following down the old root in an intertwined mass that made measuring and mapping difficult. In two cases the roots definitely reversed themselves, growing one direction in the old root and then turning about and growing back for a considerable distance parallel to the former growth. The affinity of growing roots for old root channels is probably-

accounted for by several factors including lessened
mechanical obstruction to growth, improved moisture
within the decaying organic matter, and the presence
of needed nutrients. It was noted that there was a
scarcity of branching in roots following decayed
roots, while growth in length appeared very rapid as
evidenced by the extent of the roots in young condi-
tion (that is, before typical corky bark had been
formed).

MECHANICAL OBSTRUCTIONS

Mechanical obstructions in the soil materially alter
root development and make for a lack of symmetry.
In mapping the root systems it was noted that roots
tended to grow in a straight line and that deviations
from this were usually caused by either mechanical
obstructions or the dying back of terminal portions
of the roots. Very few of the main primary roots
ever changed the direction of their growth unless
they encountered a large obstruction. Small objects,
such as other roots, were avoided by a change in
depth. Frequently these main primaries would vary
several inches in depth while growing out from the
tree in an almost straight direction.

The large number of rocks, varying in size from
gravel particles to large boulders, found in the
moraine soil at Pingree Park, would account for wide
deviation in the appearance of root systems; whereas
the remarkable uniformity of soil and lack of mechan-
ical obstructions at Hourglass Lake would indicate
symmetrical growth. The fact that these latter root
systems were not symmetrical shows that factors other
than mechanical obstructions must be considered in
accounting for root development. It was noted that
roots tended to group themselves in the layer of soil
adjacent to a large rock (Fig. 1). In a few cases
decomposing rocks were permeated by actively grow-
ing roots. This affinity of roots for rock surfaces is
probably a nutrient response, the disintegration and
decomposition of the rock material liberating nutri-
ents badly needed in this rather sterile soil.

COMPETITION

This study showed that competition may play a
major part in root development. All of the trees
excavated at Hourglass Lake were practically free
from competition, the site being nearly void of vege-
tation. It was not possible to keep competition from
being a factor at the Pingree Park site. While seed-
lings here selected for study were those that would
not compete with each other, the maze of roots, both
herbaceous and woody, throughout the soil indicated
that competition must be keen (Fig. 1). One 40-
year-old lodgepole pine, that was crowded on three
sides by more vigorous trees, was excavated to deter-
mine the feasibility of the continuance of this study
to older age classes. This tree showed clearly the
dependence of root development on competition, since
almost the entire root system extended out on the
one side where no trees were growing.

An interesting fact observed in this study is that
competition in the surface layers of soil appears to
be less keen immediately under the stem of a tree
than it is at a distance of a foot or so from the stem.
As a rule there are few absorbing roots close to the
stem of a tree and as a result there is often a small
area surrounding the stem which is relatively free
from competition. In some instances roots from
nearby trees appeared to "seek out" these uncrowded
areas, which added appreciably to the difficulties of
excavation.

In general, however, with the young trees studied
there was no very definite correlation apparent be-
tween direction and form of root growth and intensity
of competition. Frequently roots developed most
strongly where shrubby and herbaceous growth was
most dense. It was not possible to predict direction
of root growth by observing the distribution of the
plants on an area.

CHANGES WITHIN ROOT SYSTEMS

One of the major factors affecting the form of
root systems of trees is the constant change which
is taking place in the roots themselves. Unlike the
above-ground portions, which do not radically change
their form and development, root systems are con-
stantly changing. Rose (1938) studied the effects of
distortion caused by planting methods on root devel-
opment and found a tendency for the abnormality to
disappear with time. Vater (1927), working with
the root systems of large trees, found that during the
life of a tree large parts of the roots often die and
completely disappear and that then new root portions
appear which might assume forms different from
those of the dead roots. He concluded that trees may
radically change their root systems in the course of
time. In this study it was commonly found that large
portions of the root system die back and new develop-
ment takes places in some other direction. Many
of the roots growing through decaying roots would
apparently enjoy vigorous growth for a few seasons
and then die back from the tip. As a result of this
study, the author believes that root systems, except
for the tap and the main primary laterals, are com-
pletely changed many times during the life cycle.
This conclusion is in part substantiated by McQuilken
(1935), who found that nearly all the root tips be-
come dormant and many die during the dry periods
of mid-summer.

The variation in the root systems developed at the
two sites indicates that lodgepole pine has a plastic
root system which is greatly modified by changes in
the soil evironment. Pulling (1918) and Weaver
(1919) studied the flexibility of the root habits of
several species and found that there was considerable
difference between species, some exhibiting consider-
able plasticity in root development while others re-
main constant. They believe that the degree of
flexibility as regards soil penetration is an important
factor in determining the limits of distribution.

TOP-ROOT RATIO

The roots, needles, and woody portions of the
crowns of the excavated trees from the two sites

were oven dried and carefully weighed in order to determine the top-root ratio. The results are expressed graphically in Figures 5 and 6.

Considerable variation exists between the excavated trees in their top-root ratio, ranging from 0.84:1 and 4.03:1. Except for the 2-and-3-year-old classes from the Pingree Park site, all age classes have an average top-root ratio ranging from 2:1 to 3.5:1, and the average top-root ratio is 2.21:1. The average ratio for the 16-week-old seedlings raised in the laboratory on soil from the Pingree Park site was 2.3:1. The ratio for the one 40-year-old tree, which was excavated on the Pingree Park site, was 3.5:1, indicating that there may not be appreciable change in this ratio with age. Laing (1932) found that no variation with age was typical of some species, while considerable variation with age occurred in other species. All age classes from the Hourglass Lake site averaged from 1.2:1 to 2:1, with the average top-root ratio being 1.64:1.

To determine if these top-root ratios for the two sites are significantly different, the t value was calculated by the formula:

$$t = \frac{|\bar{x}_1 - \bar{x}_2|}{S'} \sqrt{\frac{N_1 N_2}{N_1 + N_2}}$$

where $S' = \sqrt{\frac{(N_1 S_2)^2 + (N_2 S_2)}{N_1 + N_2 - 2}}$,

S = standard deviation of top-root ratios,
$\bar{x}$ = arithmetic mean of top-root ratios, and
N = number of trees measured.

In this method the hypothesis is set up that there is no difference between the top-root ratios for the two sites. If t is found to be larger than a certain figure this hypothesis is rejected and a significant difference is found to exist. In the case of the top-root ratios for the two sites, the value of t is equal to 2.8084. From the table for the values of t (Leonard & Clark 1939, page 256), this is found to be very significant, exceeding even the 1 percent level. These figures clearly indicate that the top-root ratio in lodgepole pine is markedly affected by the site and substantiate the conclusions of Weaver (1919) and Haasis (1921) that the top-root ratio becomes smaller on poorer sites.

Zedebauer (1920) and Busgen and Munch (1926) studied the top-root ratio of Norway spruce (*Picea excelsa* Link). The former found that this ratio varied from 3.4:1 to 5.1:1, while the latter concluded that it always approached 4:1. These results indicate that the ratio of lodgepole pine and Norway spruce is considerably different and that the former develops a much more substantial root system.

It is interesting to note that at both sites, for trees up to 10 years old, the needles, with few exceptions, weigh more than the woody portions of the stem. As a whole, at the Pingree Park site, the weight of the roots is approximately the same as the weight of the woody portions above ground; while at the Hourglass Lake site the roots weigh approximately twice

as much as the woody portions above ground except for the 10-year-old class in which the roots average about half again as much as the stems.

PERIODICITY OF ROOT GROWTH

The roots of lodgepole pine grow continuously from the time the frost leaves the ground in the spring until it freezes again in the fall. To establish this fact, excavations were made as early as April 13, when the frost was out of the top few inches of soil, and again on November 2, when a foot of snow covered the soil and the upper few inches of it were frozen. In both of these cases, roots located in unfrozen layers were actively growing, as evidenced by the white turgid condition of the growing tips. Figures 14 and 15 were made of roots excavated on
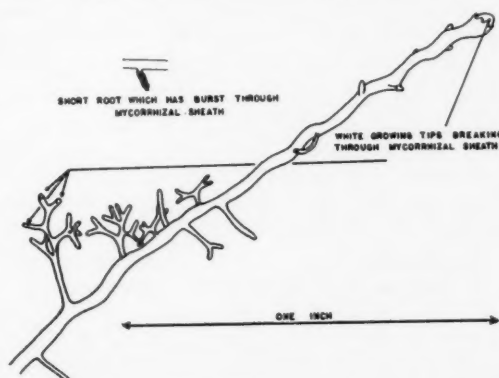
FIG. 15. Sketch of root excavated April 14, 1940.

April 13 and 14. The root excavated April 13 was from a warm southern exposure and was growing vigorously. The root excavated April 14 was on a colder site and the condition of the root indicated the very start of spring growth, as the white growing tips appeared to be just breaking through the fungal sheath which had enveloped them during the dormant period.

Studies indicate that there are no definite periods of root dormancy except for the winter rest period. This contradicts the evidence obtained by Stevens (1931) that root growth practically ceased during the summer months, as well as the conclusion of Turner (1935a) that there is a marked period of semi-dormancy from the end of June through August. On the other hand, the conclusion of McDougall (1916) that there are no summer rest periods unless accompanied by summer drought appears to be substantiated. McDougall also concludes that winter rest is due only indirectly to temperature, and that the difficulty of obtaining soil moisture rather than the direct effect of cold weather induces the dormant condition.

Laing (1932) concluded that the period of rapid root growth for all species corresponded with the period of low soil moisture and that for some species root and shoot growth appear to alternate. The data

gathered in this study do not substantiate these conclusions. Two periods of rapid root growth were noticed. One of these occurred early in the spring immediately following the thawing out of the ground —a period which preceded and accompanied the period of rapid shoot growth. At this time the ground was in a very moist condition as a result of the winter snow. The other period of rapid root growth occurred during the month of August and this did correspond with the period of lowest soil moisture.

SEEDLINGS GROWN IN LABORATORY

Certain aspects of root and top development were observed from lodgepole pine seedlings grown in the laboratory in soil from the Pingree Park site. The seeds were planted in a specially constructed box with a drop side, within which was fastened a glass panel. This panel was adjacent to the soil and through it the actual growth of the roots could be observed.

The seeds were planted January 25, 1940. The first seedling germinated Febuary 11, 1940 (18 days) and the last seedling germinated on March 8, 1940 (43 days). The number of cotyledons on each seedling were counted and the result gave a nearly perfect normal curve, the average number being four.

Number of cotyledons	Number of seedlings
2	1
3	6
4	13
5	7
6	1

Five seedlings were excavated when one week old and measured. At that time the tops averaged 1.1 inches in height, the stem 0.6 inch in height, and the roots 1.4 inches in depth. No secondary roots had appeared.

Five additional seedlings were excavated at the age of one month and measured. The tops averaged 1.4 inches in height, the stem 0.7 inch in height and the roots 1.6 inches in depth. No secondary roots had developed. The first primary leaves appeared 27 days after germination. These differ radically from secondary leaves, being single, as described by Shaw (1914).

At the age of 16 weeks, five more seedlings were excavated and studied. The measurements obtained are tabulated in Table 6.

No indications of mycorrhizae were apparent at this age, either in the form of a sheath or as hyphae within the cortical cells. It would appear that the fungal sheath is first developed during the dormant period at the close of the first season's growth.

Comparing these figures with those for one-year-old seedlings in the field, it appears that height growth is attained very early in the first season whereas root development continues throughout the growing season. It also appears from the large number of growing tips on the 16-week-old seedlings that

TABLE 6. Measurements of 16-week-old seedlings.

Tree No.	Height of stem inches	Depth of roots inches	Total length of roots in inches	Total No. lateral roots	Total No. growing tips	OVEN-DRY WEIGHTS IN MILLIGRAMS		
						Stem	Needles	Roots
110......	1.0	2.7	6.6	24	23	5	11	7
111......	0.6	3.6	8.5	24	25	3	12	5
112......	1.0	2.7	6.3	18	19	3	9	5
113......	0.6	2.9	5.6	15	15	3	11	6
114......	0.75	4.3	10.3	26	27	6	10	9
Average..	0.79	3.24	7.46	20.4	20.8	4.0	10.6	6.4

even during this first year many of the growing roots become inactive and only a small number continue the growth of the root system. This tends to substantiate the findings of McQuilken (1935) that during drought periods nearly all root tips in the upper layers of soil become dormant and many die.

ECTOTROPHIC MYCORRHIZAE[2]

The term mycorrhiza, literally meaning fungus root, refers to the intimate association of a root and a fungus. Such a compound structure is not regarded as either a root or a fungus, but as a distinct morphological organ which is analogous in structure to the thallus of lichens (Hatch 1937). Two types of mycorrhizae are generally recognized: the "ectotrophic, those in which the fungal elements are arranged intercellularly and also as a mantle over the root surface; and endotrophic, those in which the mycelium is characteristically intracellular and appears on the surface of the root as individual hyphae only" (Hatch 1937). While both types are present in Pinus, the ectotrophic are most frequent, widespread, and obvious. Melin (1922) found that short-roots growing in wet bogs and raw humus often do not form the normal ectotrophic mycorrhizae, but that the "hyphae exist exclusively in the interior of the cells and the so-called Hartig tissue, as well as the fungus mantle, is completely lacking." He terms this association a pseudomycorrhiza. None of these were observed on the roots excavated in this study.

Since Thomas Hartig classified root systems into long-roots and short-roots in 1852 (Hatch 1937) much study has been devoted to the types, structure, and functions of mycorrhizae. It is not within the scope of this investigation to enter into the controversy as to whether these fungal roots represent a symbiotic or parasitic condition, although the majority of investigators (Frank 1894; Stahl 1900; Melin 1917, 1922; Laing 1932; Hatch & Doak 1933; Hatch 1937; Mitchell, Finn, & Rosendahl 1937) have concluded that the mycorrhizal habit is essentially symbiotic and may be necessary for tree growth on certain sites.

Because of the fact that ectotrophic mycorrhizae form an integral part of the normal root system of lodgepole pine, certain studies regarding them were considered essential in order to present a rounded

[2] Hatch and Doak (1933) point out that the correct plural of mycorrhiza is mycorrhizae, not mycorrhizas.

picture of root development. The method of excavation made it possible to uncover the roots without seriously disturbing the mycorrhizae, and a rather accurate count was made of the number of these fungal roots by depth zones and quadrats on each of the two sites. Factors which influenced the distribution of mycorrhizae were also noted.

In Figure 16, the number of mycorrhizae by age
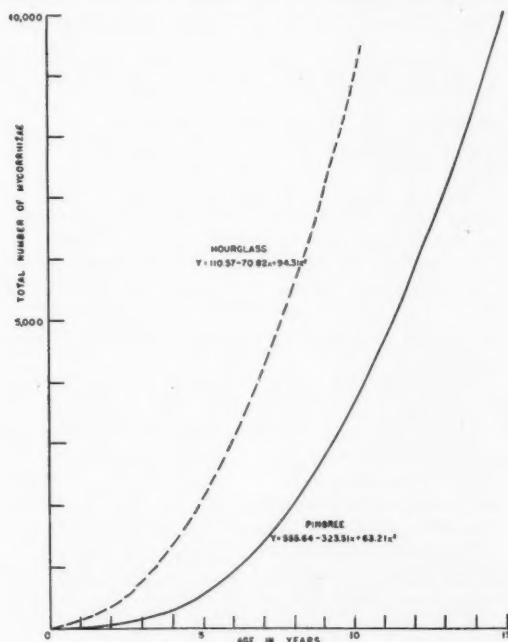
FIG. 16. Total number of mycorrhizae over age.
$$Y = A + B_x + C_{x^2}$$

classes is graphically represented for both the Hourglass Lake and Pingree Park sites. The number of mycorrhizae at the Hourglass Lake site, for any given age, is approximately double that for the Pingree Park site. This indicates a strong relationship between soil fertility and the number of mycorrhizae present and substantiates the findings of Hatch (1937) that mycorrhizae are more abundant in infertile soils.

Table 7 gives the percentage of mycorrhizae present in the different depth zones. It is evident from this table that mycorrhizae are typical of the surface layers, 89 to 97 percent appearing in the first 6 inches of soil at the Pingree Park cite and 92 to 100 percent in the same depth of soil at the Hourglass Lake site. No mycorrhizae on either site were observed at soil depths greater than 18 inches, except when the roots were growing in the channels of old decayed or decaying roots. This would indicate that mycorrhizae are dependent upon organic matter for their development, and would offer some evidence that the fungus is present in the soil before this is invaded by the growing root and that the root is in-

fected from hyphae already present in the soil rather than by hyphae carried along by the tip of the growing root. If infection resulted from hyphae carried by the root, mycorrhizae might be expected in deep layers where no decaying roots were present (Table 7).

TABLE 7. Percentage of total number of mycorrhizae present in depth zones.

PINGREE PARK						
Depth Zone	1 yr.	2 yr.	3 yr.	4 yr.	10 yr.	15 yr.
Inches						
0 - 3.....	69	82	85	92	82	56
0 - 6.....	90	94	97	97	96	89
0 - 9.....	97	98	98	99	97	91
0 - 12.....	100	99	99	100	98	93
0 - 24.....	...	100	100	...	98	96
0 - 36.....	...	...	...	...	99	98
0 - 48.....	...	...	...	...	99	99
0 - 60.....	...	...	...	...	99	99
0 - 72.....	...	...	...	...	100	100

HOURGLASS LAKE					
Depth Zone	1 yr.	2 yr.	3 yr.	4 yr.	10 yr.
0 - 3...............	89	74	80	74	69
0 - 6...............	100	99	99	92	95
0 - 9...............	...	100	100	98	98
0 - 12...............	...	...	...	100	98.5
0 - 24...............	...	...	...	...	100

McDougall (1914) stated that mycorrhizae are annual structures and this view is upheld by Masui (1927) and Aldrich-Blake (1930). McDougall (1914) also stated that the fungal sheath prohibited further growth of the fungal roots, although Masui (1926) demonstrated that this was not necessarily the case and that it was not uncommon for a mycorrhizal root to burst through the mycorrhizal sheath at the beginning of the growing season. No dead mycorrhizae were found on 10-year-old trees excavated at the Hourglass Lake site, although many of these mycorrhizae were on roots several years old. This indicates that mycorrhizae are not annual structures.

Roots excavated at the beginning of the growing season (April 13 and 14, 1940) gave further evidence that mycorrhizae are not always annual structures and that they can achieve renewed growth. Several mycorrhizal roots were active at this time as evidenced by the white tips which had burst or split the fungal sheath (Fig. 15). These mycorrhizal short-roots had been active the preceding year, and this renewed activity indicates that these particular roots were not annual. These same root systems indicated that the fungal sheath is not confined to the mycorrhizal short-roots. Growing tips of the long-roots were also completely covered by the sheath and (Figs. 14 and 15) it was clearly shown that they burst through the sheath at the time growth started. It would appear that all roots, prior to the formation of corky tissue and the death of the cortex, are subject to the formation of the fungal sheath, and rate of growth is the factor which causes short-roots

to become mycorrhizal while long-roots typically do not. Hatch (1937) has shown that the typical mycorrhizal short-roots do not grow much in length even if uninfected.

SUMMARY AND CONCLUSIONS

A study was made during the summers of 1939 and 1940 in an attempt to add to the knowledge of the growth and development of the root systems of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.).

The studies were carried out in the vicinity of the summer camp of the Division of Forestry of Colorado State College at Pingree Park, Colorado. One site was a fire lane on a gravelly sandy loam soil of glacial moraine origin; the other was in a large cut in an almost pure gravelly sand.

To determine similarities and differences in the sites certain data were recorded, such as density and composition of ground cover, elevation, slope, mechanical obstructions, and recent history. Chemical and mechanical analyses of the soils were likewise carried out.

The entire root systems of 105 lodgepole pines ranging in age from 1 to 15 years were excavated. Pressure sprayers were used to wash the roots from the soil. The entire root systems were carefully measured and mapped as they were uncovered by quadrats and 3-inch depth zones. Oven-dry weights of the roots, needles, and woody parts of the crown were determined in the laboratory.

The data were assembled and analyzed and certain important features of root development for both sites expressed graphically. Graphs were constructed by the "least squares" method which gives the most accurate curve possible among the class of curves assumed to explain the data.

The variations in top development between the two sites were not great, although top measurements were somewhat larger for the more sterile Hourglass Lake site. This was apparently the result of freedom from composition at this site.

Significant differences were observed between the root systems of the two sites in root number, length, depth, spread, and number of mycorrhizae. Roots grew much deeper at the Pingree Park site, but in all other respects root development was greater at the Hourglass Lake site.

At both sites the majority of the roots were in the upper 6 inches of soil although there was a tendency for average depth to increase with age. The lateral roots which attained the greatest extent were almost invariably shallow.

Strong correlation was found to exist between the age of a tree and the total linear length of its root system. Even stronger correlation exists between the total top height and the total linear length of the root system. As total top height is easily measured, this provides a convenient method of estimating root length.

Root systems seldom develop symmetrically and there is great variation in their extent and form.

Factors other than soil and soil moisture which were observed to affect the growth and development of roots were the presence of old roots in the soil, mechanical obstructions, and competition.

Root systems frequently undergo considerable change, even during the early years of the life of a tree. Many roots die and disappear each year and new roots are constantly developing.

The variations in root development at different sites indicate that lodgepole pine has a plastic root system.

The top-root ratio for young lodgepole pine was found to vary between 0.84:1 and 4.03:1. The difference in this ratio between the two sites was significant, averaging 2.21:1 at the Pingree Park site and 1.64:1 at the Hourglass Lake site.

Roots of lodgepole pine were found to grow continuously from the time the frost leaves the ground in the spring until it freezes in the autumn. No other periods of root dormancy were noted. There are two periods when growth is especially rapid: the first in the spring just preceding and accompanying the period of rapid shoot growth, and the second in August.

From seedlings raised in the laboratory, it appeared that most of the first year's height growth was achieved in a relatively short period following germination of the seed, while root growth was distributed throughout the growing season. The top-root ratio of 16-week-old seedlings is approximately the same as for trees from 1 to 15 years of age.

Mycorrhizal sheaths were found over the tips of lateral long-roots during the period of dormancy. These roots burst through this sheath upon resumption of growth. No cases were noted where these long-roots had their growth permanently arrested and were converted into typical ectotrophic mycorrhizae by the fungus.

The number of ectotrophic mycorrhizae at the more sterile Hourglass Lake site for any given age is approximately double that for the Pingree Park site, indicating a strong correlation between the number of mycorrhizae and soil fertility.

Between 89 and 100 percent of all mycorrhizae for each age class on both sites occurred in the first 6 inches of soil. No mycorrhizae were observed at depths greater than 18 inches below the surface except on roots growing in the channels of old roots, indicating that the fungus is probably in the soil before the coming of the root and is not carried by the root tip.

Several instances were noted where mycorrhizae had achieved renewed growth at the beginning of the growing season by bursting through the fungal sheath.

Mycorrhizae do not appear to be strictly annual structures as evidenced by the appearance of renewed growth in the spring and by the fact that no dead mycorrhizae were found on the root systems of 10-year-old trees excavated at the Hourglass Lake site.

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